

Towards modelling persistence of woodland birds: the role of genetics

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Abstract. Assessing how environmental change affects the probability of persistence of organisms requires an understanding of dispersal through, and occupation of, landscapes, and the associated demographic outcomes. Projections of differences in persistence probability can then be made under different scenarios of land-use and global environmental change. Rates and distances of dispersal, and demographic change and trajectories, are difficult to measure accurately, but genetic approaches can make major contributions. For two decades the field of molecular ecology has been providing useful life-history information relevant to population management, including key ecological attributes such as disease-resistance and thermal biology, mobility, dispersal and gene flow, habitat connectivity, the spatial and temporal scales of population processes, and demography. Genetic estimators of these factors could be employed to a much greater extent than they are currently. To facilitate this increased use, genetic estimates of functional connectivity (mobility and gene flow of organisms) and demography need to be integrated directly into decision-making processes. Population genetics is well suited to Bayesian approaches, with associated benefits including the ability to consider many factors, and estimation of error and parameter sensitivities. Genetic estimators based on the mobility and reproductive success of individual organisms and their key ecological traits can make unique contributions alongside other types of data into agent-based, spatially explicit modelling approaches of real landscape scenarios at the range of scales needed by managers. Virtually all the tools to do this exist. It is imperative that genetic samples be collected for contemporary and future analyses.

Introduction

Avian declines and the need for understanding ecological processes at landscape scales

Avifaunas worldwide are undergoing dramatic declines through human-induced loss and alteration of habitat and global environmental change. Long-term monitoring has identified significant collapses in woodland bird populations in southern and eastern Australia, including of recently common species (Mac Nally *et al.* 2009; Szabo *et al.* 2011; Watson 2011). The capacity to improve the situation depends on understanding the interaction of the natural history of species with habitat features, subsequent demographic outcomes, and critical ecological processes within a system (Kavanagh *et al.* 2007; Bowen *et al.* 2009; Selwood *et al.* 2009; Ford 2011). In one example, key drivers of extinction-proneness for some woodland birds differed among species: low dispersal ability was important for Brown Treecreepers (*Climacteris picumnus*), whereas nest predation leading to low recruitment was critical for Hooded Robins (*Melanodryas cucullata*) (Ford *et al.* 2009).

There is an increasing appreciation that demographic processes for organisms must be considered at different spatial scales including large 'landscape mosaics' of patches of habitat in matrices of various land-use types (Cushman and McGarigal 2004; Bennett *et al.* 2006). Fortunately, patch-scale habitat data are increasingly available at landscape scales, such as mapping vegetation-cover down to single trees using high-resolution satellites (Levin *et al.* 2009). The size and quality of a patch can

affect population sizes and migration rates, whereas the intervening matrix may affect success of migrants (Balkenhol *et al.* 2009a, 2009b). For example, White-browed Treecreepers (*Climacteris affinis*) were absent from patches >3 km from other patches in agricultural land, in contrast to >8 km in native vegetation. At much larger scales, a threshold was detected wherein the species was absent from 100 km² landscapes with <15–25% tree cover (Radford and Bennett 2004).

Research at landscape scales has been conducted only infrequently owing to its challenges, but has led to important insights. Radford and Bennett (2007) developed species-specific models examining the influence of landscape-mosaic attributes on the incidence of 58 species of woodland-dependent birds in 24 agricultural landscapes (each 100 km²) in south-eastern Australia. For 27 species, habitat extent was a positive influence. Thirty species responded to landscape composition, geographical location was important for 19, and habitat configuration influenced 13. Impacts of habitat fragmentation were detrimental and for some species, including Weebill (*Smicrornis brevirostris*) and Spotted Pardalote (*Pardalotus punctatus*), greater structural connectivity supported larger populations. The same research program revealed variable responses among species (Radford *et al.* 2005).

Aim of this paper

This paper reviews the contributions of genetic approaches to management of natural populations, with emphasis on woodland

birds. Special emphasis is given to the estimation of dispersal, functional connectivity of habitat (i.e. how habitat supports biotic mobility and gene flow), and projections of demography and population persistence.

Two ends of a continuum: fitness genetics and molecular population biology

Genetic information provides a spectrum of input into conservation management, from fitness genetics (how genetic variation has an impact on the fitness of individuals and population persistence), through to molecular population biology (how genetic variation can provide information about population processes and trajectories).

Fitness genetics

Negative impacts of inbreeding are large and fast-acting (Keller and Waller 2002): the immediate chance of death of an offspring from a vertebrate full-sib mating, through inbreeding 'unmasking' lethal genes, approaches 50%. Harmful effects of inbreeding are virtually ubiquitous, and cause major fitness and demographic declines in free-living populations of birds (Keller *et al.* 1994; Keller 1998; Markert *et al.* 2004). Important functions including disease-resistance, reproduction and population recruitment are damaged disproportionately by inbreeding (Keller 1998; Reid *et al.* 2003). It is thus unsurprising that inbreeding through population contraction leads to increased extinction risk (Saccheri *et al.* 1998; Nieminen *et al.* 2001; Frankham 2005a; O'Grady *et al.* 2006). A decline in habitat quality may contribute to 'extinction debt' before demographic stochasticity finally delivers the *coup de grâce* (Ford *et al.* 2009; Szabo *et al.* 2011), but inbreeding depression may often drive demographic decline. It is detectable by genetic approaches, and is potentially reversible.

Inbreeding depression can be reversed with gene flow. Experimental 'genetic rescue' was effected for isolated populations of Greater Prairie-chickens (*Tympanuchus cupido*). These populations had experienced long-term demographic decline through inbreeding depression, with hatching rates falling from 93% to 56% between 1935 and 1990 (Bouzat *et al.* 1998a, 1998b; Westemeier *et al.* 1998). The decline continued after removal of threats and improvement in habitat quality, but was rapidly reversed by the introduction of genes from neighbouring sources.

Longer-term harmful effects of reduced genetic variation include lowered evolutionary responsiveness (Frankham 2005b). The effective population size (N_e , heuristically the number of individual-equivalents making a full contribution to the next generation) at which natural selection would be subsumed by random genetic drift, that is evolution on a trait would cease, occurs when the selection coefficient, $s < 1/(2N_e)$. Thus, evolution on a typical vertebrate immunity-gene with $s \sim 1\%$, stops when N_e is below ~ 50 , at which point critical genetic variation is lost as if it is of no benefit. Since census population sizes for wildlife are on average $\sim 10N_e$ (Frankham 1995), populations of >500 or so are required for effective evolution of even the most important functional genes. Census sizes of thousands are required for genes under weaker, but still important, selection.

The foregoing underlines the importance of maintaining large populations of natural organisms that experience levels of gene

flow similar to that under which they evolved. If genetic factors in population persistence are ignored, extinction risk will be underestimated and inappropriate recovery strategies may be applied (O'Grady *et al.* 2006; Willi *et al.* 2006).

An end to the false dichotomy between ecological and genetic factors in population persistence

The negative impacts of population reductions have sometimes been dichotomised as ecological and genetic but they are inseparable and we must focus on effective conservation solutions, which so often incorporate genetics (Johnson *et al.* 2009). Despite its undoubted, legally-recognised, efficiency (Fallon 2007; Bean 2009), molecular population biology remains underutilised in ecological management, mainly for cultural, institutional and historical reasons (Waples *et al.* 2008; Johnson *et al.* 2009; Vernesi and Bruford 2009).

Population persistence is dependent on functional genetic variation, usually correlated with effective population sizes and gene flow (Reed and Frankham 2003). Thus, understanding population persistence can benefit from molecular estimates of connectivity, dispersal and gene flow, effective population sizes and demographic trajectories (see below).

Molecular population biology in managing populations for persistence

Introduction to molecular population biology

The extensive contributions of molecular population biology to ecological management have been reviewed elsewhere (Pearse and Crandall 2004; DeYoung and Honeycutt 2005; Scribner *et al.* 2005; Excoffier and Heckel 2006; Rollins *et al.* 2006; Selkoe and Toonen 2006; Sunnucks and Taylor 2008; Waples *et al.* 2008; Balkenhol *et al.* 2009a; Simmons *et al.* 2010). The main focus here will be on factors associated with understanding population persistence.

The Bayesian revolution in molecular population biology

Bayesian statistical approaches are becoming central in environmental science (Beaumont and Rannala 2004; Clark 2005). Bayesian inference is convenient for models with many interdependent parameters, allows incorporation of background information, can accommodate uncertainty, and includes variability without recourse to inefficient summary statistics. Likelihood problems that are otherwise too complex can be addressed using Markov Chain Monte Carlo (MCMC) techniques.

Molecular population biology is well suited to this Bayesian environment (Beaumont and Rannala 2004). Variability among genetic loci can be incorporated through Bayesian models for which there is no feasible classical counterpart. Importantly, Bayesian approaches can estimate what is directly of concern, avoiding unnecessary intermediate statistics (Hadfield *et al.* 2006). Additionally, Bayesian approaches overcome limitations of alternative approaches as revealed by tests of reliability (Latch *et al.* 2006; Chen *et al.* 2007; Selkoe *et al.* 2008; Balkenhol *et al.* 2009b).

Coalescent theory, which describes mathematically the properties of samples of genes from their mutational processes and genealogical relationships (Kingman 1982) forms the basis for

likelihood calculations in genealogical models, and has allowed the use of Bayesian approaches to infer demographic history from genetic data (Beaumont and Rannala 2004). The probability of coalescence (backwards merging to a single common ancestor) of neutral genes depends on effective population size, population subdivision and the passage of generations, and is an extremely useful simulation environment for complex population histories.

The fundamental sources of information in molecular population biology

Population biology information resides in genetic data through variation at genetic markers within and among individual organisms (Sunnucks 2000). Because individuals share genetic similarity through common descent, genetic similarity can reveal diverse elements of population biology and history. This information is accessed via two complementary main routes (Stow *et al.* 2001), as follows.

Indirect genetic methods are based on theoretical relationships between attributes estimated from population samples, such as differences in allele frequencies, and parameters of interest such as number of migrants, effective population sizes, and demographic change. These approaches tend to rely on simple models and assumptions. Being based on population frequencies, which have some inertia, indirect genetic measures reflect cumulative effects of biological processes over many generations.

In contrast, direct genetic methods are based on genotypes of individuals rather than on allele frequencies of samples, and link individuals to their provenance (parents, population, etc.). The population is a critical demographic unit, yet it is extremely difficult to identify by non-genetic approaches. Being based on individual genotypes that turn over in every sexual generation, direct genetic approaches respond within only one or a few generations. A key development is statistical ‘assignment tests’ (Manel *et al.* 2005). With sufficient samples and genotypic power, individuals can be correctly assigned to populations of origin (Paetkau *et al.* 2004). This information can be applied, for example, to measuring and monitoring populations in disturbed and natural landscapes by enumerating migrants, whether they breed, and, with substantial sampling, may produce matrices of dispersal distances and directions. Direct genetic approaches are profoundly suited to agent-based, spatially explicit modelling for biodiversity management, for which there is an urgent need (Balkenhol *et al.* 2009a).

What molecular biology can do for population management

Understanding fundamental biology and ecology

Knowledge of avian biology has been revolutionised by high-resolution genetic techniques, starting with DNA fingerprinting (Burke and Bruford 1987). For example, dominant male Superb Fairy-wrens (*Malurus cyaneus*) hold large harems, but parentage–paternity analysis shows that they obtain only a small proportion of within-group fertilisations (Double *et al.* 2005). In contrast, a single congeneric, the Purple-crowned Fairy-wren (*M. coronatus*), is predominantly monogamous (Hall and Peters 2009). Similarly, genetic research has greatly enhanced our understanding of dispersal, demographics and how species re-

spond to altered landscapes (e.g. meliphagid miners (*Manorina* spp.), Pöldmaa *et al.* 1995, Painter *et al.* 2000; Australian Magpies (*Gymnorhina tibicen*), Baker *et al.* 2000, Durrant and Hughes 2005, 2006; Horsfield’s Bronze-Cuckoo (*Chalcites basalis*), Langmore *et al.* 2007; White-winged Choughs (*Corcorax melanorhamphos*), Beck *et al.* 2008). Such information is important for developing parameters for population models.

Facilitating specific direct management interventions

Internationally, genetic approaches have been important in focussing direct management interventions in captive and wild populations of species of conservation concern. Examples include genetic management and monitoring of captive breeding programs for re-release (e.g. Mauritius Kestrel (*Falco punctatus*), Nichols *et al.* 2001; South Island Takahe (*Porphyrio hochstetteri*), Grueber and Jamieson 2008), and testing the provenance of reintroduction stocks (Greater Prairie-chicken; Palkovacs *et al.* 2004). Such approaches have rarely been resourced and applied to Australian biota, although Rollins *et al.* (2006) give an overview for managing invasive species.

Monitoring of populations and wildlife utilisation

In situations with regulated management of wildlife, genetic identification of individuals, sexes and species are useful for many purposes including population monitoring, detection of illegal or inappropriate use of wildlife, and managing harvesting and by-catch (DeYoung and Honeycutt 2005; Scribner *et al.* 2005). Pillay *et al.* (2010) developed microsatellite markers for detecting illegal trade in the critically endangered Cape Parrot (*Poicephalus robustus*). Although genetic monitoring has been rare in Australian birds, the potential is exemplified by work on Shy and White-capped Albatrosses (*Thalassarche cauta* and *T. steadi*), which revealed different vulnerability of classes of individuals, populations and species to mortality caused by fisheries (Abbott *et al.* 2006).

The robust nature of DNA under many conditions of preservation means that small amounts of poor-quality material, such as shed feathers, can yield sufficient DNA for identification of individuals, their sex, population of origin, species and other categories (e.g. Powerful Owl (*Ninox strenua*); Hogan *et al.* 2008). If suitable samples exist, time-series from museum specimens may be used to assess temporal population changes (e.g. Bouzat *et al.* 1998b).

Identification of management units

Designated taxonomic units are often a pre-requisite of isolated protection of wildlife (Scribner *et al.* 2005; Laikre *et al.* 2009). What comprises an important biological unit can be contentious (Crandall *et al.* 2000; Waples and Gaggiotti 2006). Genotypic clustering (see ‘Genetic analysis of population structure’, below) makes delimiting populations quite straightforward, but their functional significance demands additional consideration. Long-recognised morphological features associated with species and subspecies may (or may not) be of functional significance but may nonetheless trigger expenditure of conservation resources. Genetic approaches have shown that subspecies boundaries are often discordant with evolutionary

history or function, or both. Although such assessments are sometimes based for pragmatic reasons on only mitochondrial DNA (mtDNA), well known to be risky (for Australian birds, see Joseph and Omland 2009), there are many cases where morphology, other traits and geography do not mirror evolutionary lineages (e.g. Palm Cockatoos (*Probosciger aterrimus*), Murphy *et al.* 2007; Australian Magpie, Toon *et al.* 2007). Genetic approaches give new insights into some long-standing questions of taxonomy and evolution. For example, the Crimson Rosella (*Platycercus elegans*) ring species appears to be driven by geographically differentiated selection and drift, and is not the simple ring as traditionally thought (Joseph *et al.* 2008).

Evolutionary relationships among population units – phylogeography

Phylogeography, the study of how evolutionary lineages are distributed in geographical space and time, makes important contributions to wildlife management (Joseph and Omland 2009). Its role in identifying and mapping the distribution of biodiversity was outlined above (see 'Identification of management units'). When done for suites of organisms, this can identify areas of endemism harbouring and generating biodiversity, useful for determining priorities for conservation (Knowles 2009; Rosauer *et al.* 2009). This can be put in the context of understanding the impacts of environmental change (Carnaval *et al.* 2009; Hofreiter and Stewart 2009).

Phylogeographic analyses can be applied to assess functional significance of local morphological forms. To test whether genetic drift could explain the morphological divergence observed between Zebra Finch (*Taeniopygia guttata*) subspecies, Lande's N_e^* statistic (an estimate of the genetic population size at which drift alone would explain the observed morphological divergence) was assessed alongside estimates of neutral marker and morphological divergence (Balakrishnan and Edwards 2009). Natural selection on traits, not just drift, was inferred to have been important during the ca. 1.9 million years of divergence between Zebra Finches of Australia and the Lesser Sunda Islands. Similar effects were seen for island Silvereyes (*Zosterops lateralis*) (Clegg *et al.* 2002), and European Pied Flycatchers (*Ficedula hypoleuca*) (Lehtonen *et al.* 2009).

Phylogeography underpins evaluations of long-term demographic change (Johnson *et al.* 2009). For example, Balakrishnan and Edwards (2009) reconstructed the history of divergence and demography between subspecies of Zebra Finches. They concluded that both subspecies have experienced population growth during and since divergence, with non-zero but very low gene flow between them, more from the mainland to islands than vice versa.

When applied to multiple, co-distributed taxa, phylogeography can reveal population and evolutionary trends in ecological communities (Garrick *et al.* 2008). Because genetic divergences carry the signature of contemporary impacts as well as historical ones, historical demography underpins the ability to distinguish between gene flow among populations and divergence in isolation among recently subdivided populations, critical to understanding current connectivity (Pavlacky *et al.* 2009; Zellmer and Knowles 2009).

Identifying and understanding evolution of key traits associated with environmental change

Understanding the key traits and their evolution in wildlife is necessary for predicting contemporary responses to environmental change (McRae *et al.* 2008; Pimm 2008; Norgate *et al.* 2009; Kearney *et al.* 2010). Two intersecting areas of research exemplify the significance of evolutionary responses of woodland birds: life-history changes associated with global climate change, and rapid evolution of dispersal in the face of habitat fragmentation. In Great Tits (*Parus major*), spatially differentiated patterns of dispersal drive evolution of traits such as body size at very local scales and over periods of 36 years or less (Garant *et al.* 2005). A subsequent major analysis indicated strong and rapid shifts in life-history characteristics, such as earlier laying during recent, warmer times (Garant *et al.* 2008). The fact that climate and habitat fragmentation interact emphasises the importance of understanding mechanisms of population processes, not just patterns (Kearney and Porter 2009).

Life-history shifts that are consistent with being responses to climate change have also been detected in Australian birds. Body size in eight species of Australian passerine has declined since 1950, so that southern populations now have body sizes typical of northern populations before 1950, equivalent to a 7° shift in latitude (Gardner *et al.* 2009). Since the decline was 1.8–3.6% of wing-length, and larger birds typically fly further, this suggests a key mechanism linking climate adaptation and dispersal ability.

Rapid evolution of dispersal traits can have direct demographic consequences. Western Bluebirds (*Sialia mexicana*) are expanding into the range of Mountain Bluebirds (*S. currucoides*), owing to logging of forests. Individuals with heritable high aggression are generally also more dispersive, so there is strong selection for aggression during colonisation (Duckworth and Badyaev 2007). Thereafter there is selection against dispersal because aggressive males provide almost no parental care, with fatal results for many offspring. These effects seem to be general. Evolution of dispersal strategies have major impacts on rate and mode of range-shifting (Dytham 2009), and variance in dispersal distance is critical in landscape-scale population connectivity and recolonisation (Trakhtenbrot *et al.* 2005; Tittler *et al.* 2006; van Houtan *et al.* 2007).

Genetic analysis of population structure

Molecular population biology can make major contributions to areas of population biology that are otherwise very challenging: population structure, dispersal and gene flow, and habitat connectivity and demographic estimation. Perhaps the most straightforward of these is identifying patterns of spatial population structure, important for maintaining populations, and for focusing pest control and eradication (Abdelkrim *et al.* 2005; Waples *et al.* 2008). Some recent in-depth reviews of spatial genetic approaches include Manel *et al.* (2003), Holderegger and Wagner (2008), Storer *et al.* (2007) and Guillot *et al.* (2009). Excoffier and Heckel (2006) review 13 commonly used programs: Arlequin, FSTAT, GDA, Genepop, Genetix, MSA, SPAGeDi, Hickory, Structure, BAPS, Geneland, DnaSP and MEGA.

Classic approaches to identifying population genetic structure were based on differences in allele frequency at genetic loci among population samples. Summary statistics included mea-

asures of genetic distance adapted for different purposes, and the commonly used standardised measure of difference, Wright's F_{ST} on which much of core population genetics theory is dependent. Although they remain useful, approaches based on F_{ST} have significant limitations (e.g. Neigel 2002; Guillot *et al.* 2009). Such is the embedded nature of F_{ST} -like measures in the field that even well-known biases often go uncorrected. For example, G_{ST} underestimates population differentiation as within-population diversity increases, but it remains rare to apply Hedrick's (2005) simple correction, G'_{ST} (Heller and Siegmund 2009).

One fundamental limitation of F_{ST} -like measures is that individuals must first be put into groups among which differentiation is assessed. This may be somewhat circular, since grouping requires assumptions about spatial population genetic structure. Assuming that groups actually exist, this circularity can be overcome by individual-based assignment and clustering approaches, where multiple loci are scored to make a genotype array per individual and these genotypes used to cluster individuals into genetic groups (Paetkau *et al.* 2004; Manel *et al.* 2005). These tests can have the power to detect population genetic structure even when F_{ST} is very low (Latch *et al.* 2006), particularly the modified contingency test of Waples and Gaggiotti (2006). They can be conducted under alternative paradigms for different purposes (Manel *et al.* 2005). For example, in cases where many potential source locations for an individual are likely to be unsampled (as will often be true for woodland birds because of large species geographical ranges, mobility and population sizes), a test that asks whether an individual is locally born or not will be more appropriate than one that tries to assign an individual to a location of origin from an array of options. An assessment of the effectiveness of methods for detecting populations and identifying barriers to gene flow of three commonly used programs – Structure, TESS and Geneland – was conducted by Chen *et al.* (2007) (although see Guillot *et al.* 2009 for qualifications). In an empirical example, Structure, BAPS and TESS gave different insights into of the population structure of Black-capped Vireos (*Vireo atricapilla*): the latter two incorporated geographical information and detected population differentiation not evident with Structure (Barr *et al.* 2008). Among the many advantages of individually based approaches is their ability to account for unexpected complexity, such as the association between higher levels of individual genetic diversity and earlier settlement of returning migrant Tree Swallows (*Tachycineta bicolor*) (Porlier *et al.* 2009).

Landscape genetics: relating spatial genetic patterns to landscape features

Usually in ecological management it will be useful to assess spatial and temporal patterns in genetic data, and relate them to landscape features. Within the last decade, these approaches have developed very rapidly and been dubbed landscape genetics (Manel *et al.* 2003; Storfer *et al.* 2007; Holderegger and Wagner 2008; Balkenhol *et al.* 2009a, 2009b).

With classic allele frequency data, the spatial scale of population organisation is often assessed by hierarchical analyses such as analysis of molecular variance (AMOVA, a molecular analogue of analysis of variance (ANOVA); Excoffier *et al.* 1992) that partition genetic differences among samples into levels of

organisation (e.g. sites within regions or dates within time-series). Alternative approaches include tests for or among spatial patterns such as isolation-by-distance. Pairwise geographical distances between sites may be tested for linear correlation with pairwise genetic distances, often with Mantel tests. When relationships are non-linear, spatial autocorrelation (most often conducted within GenAlEx 6 (Peakall and Smouse 2006)) is more appropriate, since it partitions the analysis into different distance-class bins, and can reveal different answers at different spatial scales. Spatial autocorrelation can be conducted with population samples or individuals as the units, but comparing the two can be useful in understanding temporal changes in population patterns (Stow *et al.* 2001). Spatial autocorrelation is typically applied as a one-dimensional analysis, mainly because the two-dimensional version is difficult to apply and not well catered-for in software. Two-dimensional (2-D) spatial autocorrelation was used on Superb Fairy-wrens to detect 'hot-spots' of genetic similarity driven by locally successful male breeders (Double *et al.* 2005).

The approaches introduced above, except 2-D spatial autocorrelation, are about spatial scale and pattern, not explicit space. Individually based approaches are used to define spatially explicit population structures (e.g. in Structure; Pritchard *et al.* 2000). There are two main outcomes of this suite of analyses: (1) the number of population units is assessed statistically; and (2) each individual is attributed to genetic population(s). Notwithstanding the latter, these approaches are different in emphasis than assignment tests, which focus on the statistical attribution of individuals rather than the discovery or delimiting of groups (Manel *et al.* 2005).

The clustering approaches described above assume some degree of distinctiveness among groups that may not exist. Thus clustering may be inappropriate without accounting for isolation-by-distance (Cushman *et al.* 2006; Jombart *et al.* 2008; Guillot *et al.* 2009). An alternative is to place individuals in a genetic continuum, for example by using spatial principle components analysis (sPCA) (Jombart *et al.* 2008). Methods based on continuous genetic surfaces were able to detect simulated landscape genetic structure five or more generations post-vicariance at migration probabilities ≤ 0.10 , even when population differentiation was very low ($F_{ST} \geq 0.00015$) (Murphy *et al.* 2008). The approach was also able to detect simultaneous impacts of landscape features and isolation-by-distance.

Population genetic structure can arise through stochastic and deterministic processes, the interaction of species biology with natural and anthropogenic habitat features, and occur at different spatial and temporal scales. It is very often desirable to assess the association between landscape and habitat features and population processes, that is the relationship between structural and functional connectivity. Given the many contributors to population genetic patterns, testing these relationships requires a careful, multifaceted approach, preferably testing strong prior predictions. Although not straightforward, genetic approaches are very powerful in this context, and often the only feasible way to address the issues.

Specific barriers to mobility and gene flow of an organism through a landscape are assessed in two main ways using genetic data. One approach is a hypothesis-testing approach to whether given habitat structures explain observed genetic patterns (Balkenhol and Waits 2009; Simmons *et al.* 2010). Ideally

before-and-after sampling is used, but when this is not possible, genetic estimators of prior conditions may suffice. Alternatively, in the absence of clear prior hypotheses or before-and-after samples, genetic data can be examined for patterns, yielding candidates for subsequent hypothesis-testing (Guillot *et al.* 2009 and below). Methods are emerging to disentangle the effects of barriers from underlying isolation-by-distance (Paquette and Lapointe 2009), and statistical approaches can be applied to the congruence of genetic breaks with hypothesised barriers (Garrick *et al.* 2008).

It may be critical in formulating restoration efforts and future landscape management to gain a quantitative understanding of the time-scale over which genetic discontinuities develop. Similarly it can affect choices among management actions to what extent human impacts on landscape features contributed to genetic structure. Though it is rare to have pre- and post-influence samples for comparison, genetic data may nevertheless resolve the time-scale of discontinuities because hereditary processes can generate temporal signal. For microsatellites, almost ubiquitously available in landscape genetics studies, one good approach is the $R_{ST}/p R_{ST}$ test for whether evolutionary or recent genetic drift time-scales contribute to population differentiation (Hardy *et al.* 2003; Beckman *et al.* 2007). A more sophisticated population genetic modelling approach can be used to compare different migration scenarios quantitatively (e.g. Lada *et al.* 2008). Diverse software is available, including EASYPOP, MS, METas.IM, Geneland, IBDSIM, DIYABC and SPLATCHE (Balloux 2001; Currat *et al.* 2004; Balkenhol *et al.* 2009b; Guillot *et al.* 2009).

The foregoing focussed on specific strong barriers to mobility and gene flow, but it is important also to understand filtering effects in landscape mosaics. The unresolved debate about the importance of habitat corridors is made redundant by considering continuous landscape resistance (Cushman *et al.* 2009).

Landscape genetics seeks to explain population genetic patterns with environmental variables and so evaluate the importance of landscape features in mobility and gene flow. One broad approach to this is via correlations between the environmental differences between pairs of locations and their corresponding genetic distances, accounting for simple geographical distance (e.g. Geffen *et al.* 2004). In least-cost path (LCP) approaches, costs or resistances to movement through different habitat types are hypothesised, and the shortest LCP is identified that would minimise resistance to mobility between two points if these ideas were true. Validity of the LCPs is assessed with the corresponding genetic distances (Storfer *et al.* 2007). In one particularly elegant study, Cushman *et al.* (2006) tested 110 resistance hypotheses for their ability to explain genetic data (dissimilarities among all individuals based on nine microsatellite loci) in Black Bear (*Ursus americanus*). Land cover, slope, elevation, roads, geographical distance, and a putative river valley barrier were tested by causal modelling for importance, and the outcomes used to map dispersal routes for large-scale conservation planning (Cushman *et al.* 2009). Such large numbers of landscape models call for strong prior hypotheses or at least data-mining to detect patterns for further testing (Balkenhol *et al.* 2009b).

Least-cost paths make biologically unrealistic assumptions, such that dispersing organisms have perfect knowledge of their environment, including parts they have not visited, and only optimal paths are used. These shortcomings are addressed by the

concept of isolation-by-resistance (IBR) and the associated software Circuitscape, which applies electrical circuit theory to integrate estimated biological mobility over all possible paths between points (McRae and Beier 2007). Under IBR, mobility is modelled in inverse proportion to the resistance offered by the habitat along all routes between points. Resistance surfaces based on prior ideas or data are supplied, and the more those surfaces explain the genetic data, the better they have identified factors affecting dispersal and gene flow. IBR can explain more of the variation in genetic patterns than geographical distance or LCP (McRae and Beier 2007). This area will continue to develop, for example more exploration of the merits of different measures of genetic distance may be beneficial, and full Bayesian models for the fit of surfaces to genetic data are likely to be far more revealing than Mantel matrix correlations. Circuitscape is becoming a common tool for production of cost-distance matrices which can be used as part of the input for demographic and population genetic modelling. For example, it is accepted by CDPOP, an individually based, spatially explicit, population genetic simulator that incorporates a very flexible and detailed demographic model, and can be used to investigate relationships between landscape resistance surfaces, gene flow and population genetic patterns in a computationally efficient manner (Landguth and Cushman 2010).

Estimating dispersal

Why is it important to measure dispersal? Individuals moving permanently from their place of origin and then reproducing has important consequences in terms of demography and gene flow (Broquet and Petit 2009). Individually based, spatially explicit demographic modelling tied very closely to intensive field observations suggests that mobility rules are critical in demographic trajectories of populations (e.g. Brown Treecreepers; Cooper *et al.* 2002a).

Population and landscape management presents a critical need for data on dispersal of organisms (Fahrig 2007). Knowledge of dispersal rates, mean dispersal distances, variances and long-distance dispersal are necessary to understand the relationship between structural and functional habitat connectivity, outcomes of dispersal and population persistence. The importance of quantifying dispersal, and how it changes with habitat alteration, is underpinned by recent research from the Biological Dynamics of Forest Fragments Project near Manaus, Brazil, testing the widely held belief that birds disappear from tropical forest fragments because they are poor dispersers (van Houtan *et al.* 2007). Contrary to popular assumptions, species prone to disappear from patches were generally good dispersers before habitat alteration, but mobility was curtailed by habitat isolation, except that they tended to emigrate from small patches. On the other hand, patch-persisting species were generally less mobile in pre-alteration landscapes and avoided crossing gaps, but after fragmentation they tended to disperse further. Overall, dispersal kernels were characterised by some very long-distance movements, counter to preconceptions.

The role of genetics in estimating dispersal rates and distances. Detailed measurements of how organisms use habitat features, such as scattered trees or riparian strips, are critical for analyses of functional landscape connectivity. At this level of detail, field observations are very effective if logistically viable.

For example, Grey Shrike-thrushes (*Colluricincla harmonica*) and White-throated Treecreepers (*Cormobates leucophaea*) were challenged to move, using playback of vocalisations (Robertson and Radford 2009). They showed strong resistance to crossing gaps, although Grey Shrike-thrushes used scattered trees. Radio-transmitters can now weigh as little as 0.6–0.9 g and be suitable for monitoring the mobility of birds weighing only a few tens of grams for ~2–5 weeks over scales of kilometres (Doerr *et al.* 2011).

Unfortunately, for many organisms and under many circumstances, despite technical advances, estimating dispersal by field approaches remains labour-intensive, difficult and expensive, so sample sizes are usually small (Tittler *et al.* 2009; Simmons *et al.* 2010). Stable isotope approaches are improving, but currently are of limited use in measuring dispersal (Brattström *et al.* 2008; Inger and Bearhop 2008).

Genetic methods are powerful tools in estimating dispersal rates and distances and have an essentially irreplaceable ability to put dispersal rates in a temporal context – direct methods assess dispersal over one or a few generations, indirect methods assess dispersal over one to thousands of generations depending on effective population size and migration rates (Broquet and Petit 2009). Most importantly, genetic approaches are irreplaceable in their ability to measure genetically effective dispersal, that is that dispersal leading to gene flow. In a striking example, intensive field techniques showed that Florida Scrub-jays (*Aphelocoma coerulescens*) dispersed further in fragmented than continuous habitat, but that gene flow was less effective in long-distance dispersers (Coulon *et al.* 2010).

Molecular approaches to estimate dispersal may be dichotomised as indirect and direct (see ‘Fundamental sources of information in molecular population biology’ above, and elaborated below). Most direct methods measure all dispersal, whereas indirect methods measure only genetically effective dispersal (Broquet and Petit 2009). Currently, two kinds of dispersal distance may be estimated genetically: distance travelled by male gametes from production to fertilisation sites, and distance travelled by offspring between birthplace and location of first reproduction (natal dispersal) (Broquet and Petit 2009). (A third category, breeding dispersal, can be inferred from genetic approaches including repeated non-invasive genotyping, although this is intensive and has been conducted only at limited scales (Walker *et al.* 2008a).) These approaches yield discrete data about individuals that can be used as such or assembled into dispersal kernels for populations or groupings, for example genetic approaches are very effective in quantifying sex-biased dispersal (e.g. Beck *et al.* 2008). Other methods infer summary parameters: of particular significance is the average dispersal distance σ (see below on the method of Rousset 2000 and Watts *et al.* 2007).

Genetic techniques for estimating dispersal are not a panacea. However, they present some very significant benefits and opportunities, and in many situations will be the most effective and inexpensive tools for assessing mobility, and even high-intensity fieldwork is far more effective and accurate when molecular genetic approaches are integrated (Hansson *et al.* 2004). Generally, field studies are expected to underestimate dispersal rates owing to unsampled life stages, rare or long-distance dispersal and limits on ability to observe movements. Genetic approaches

help overcome these limitations, not least because genetic methods can estimate mobility from a single sampling or capture per individual. Where repeat sampling is desirable, non-invasive genetic approaches are available for many species and can lead to otherwise unattainable insights (Banks *et al.* 2003; Walker *et al.* 2006, 2007, 2008a, 2008b), although an analogue to tape-trapping hairs from burrowing mammals is not currently applicable to many birds.

As with most approaches in science, estimation of genetic mobility experiences a trade-off between the intensity of sampling and the precision and sophistication of the answer. There are three main variables: number of independent genetic markers (loci), number of individuals per location, and intensity of sampling. For many approaches, published simulations assess the trade-offs (e.g. Bernatchez and Duchesne 2000). Although screening large numbers of loci can be advantageous and is becoming increasingly quick and inexpensive, in many cases the benefit flattens out at around a highly feasible 10–20 (e.g. for population divergence of Red-backed Fairy-wrens (*Malurus melanocephalus*); Lee and Edwards 2008).

The theoretical underpinnings for applying genetics to estimate population parameters, including dispersal, are long-established, but have not penetrated population biology thoroughly. Empirically, genetic and field-based estimates of dispersal that can be compared are usually well correlated (Sumner *et al.* 2001; Berry *et al.* 2004; Stow and Sunnucks 2004a, 2004b; Double *et al.* 2005; Watts *et al.* 2007).

Indirect genetic approaches to measuring effective dispersal. Classic population genetics produced approaches to estimate $N_e m_e$ – the effective population size multiplied by the fraction of migrants (i.e. the number of genetically effective migrants per generation). A core approach is based on the theoretical relationship between F_{ST} and $N_e m_e$. This relationship is strongly non-linear so has low power over much of its range, and assumes population genetic equilibria and adherence to the island model (although it is quite robust to violations; Broquet and Petit 2009). An additional fundamental issue for demographic projection is that m_e is generally of more interest than $N_e m_e$, making it necessary to estimate N_e , which may not be straightforward (Waples and Gaggiotti 2006; Lowe and Allendorf 2010). The kind of markers used to estimate F_{ST} needs consideration, since this will impact the absolute values from which $N_e m_e$ is estimated (Heller and Siegismund 2009). Some methods designed to estimate m_e from F_{ST} have been derived, but require temporally repeated sampling, in some cases, before and after reproduction (Broquet and Petit 2009).

The foregoing was based on the island model. Approaches also exist under isolation-by-distance population models, based on the relationships between genetic structure and dispersal (Rousset 1997). The classic unit of population structure is Wright’s ‘neighbourhood’, a physical area containing several individuals (the neighbourhood size) of sufficient mobility to potentially unite gametes within a single generation. A straightforward interpretation of neighbourhood as the size of a ‘panmictic unit’ should be avoided, but it remains a convenient metric of the balance between local genetic drift and gene dispersal within continuous populations (Vekemans and Hardy 2004) and is used as a dispersal parameter, assuming stable densities (Epperson 2005; Broquet and Petit 2009).

Estimates of genetic neighbourhoods have been made frequently in the conservation literature, usually to understand the spatial scale of population function in the context of habitat spatial organisation, for example, identifying the minimum population size for which it is useful to estimate effective population size. If a functional population unit is spread over several habitat patches, conservation actions to maintain connectivity might be given a higher priority than if a single patch contained one or more neighbourhood (e.g. highly localised frogs (Driscoll 1999) v. a wide-ranging mammal (Lodé and Peltier 2005)).

Because neighbourhood size is a factor in the increase in genetic differentiation with geographical distance, it can potentially be estimated from spatial genetic data (Rousset 1997). Neighbourhood size in two-dimensional habitats, assuming Gaussian distribution of dispersal, may be calculated as $4\pi D\sigma^2$, where D is a measure of population density (the genetically effective time-scaled population density, equal to the rate of coalescence per unit time and per surface unit; Watts *et al.* 2007), and σ^2 is a metric of dispersal (the mean axial square of genetically effective parent-offspring dispersal rate per generation; see Broquet and Petit 2009 for a clear illustration). Thus from neighbourhood size, dispersal rate can be estimated if density is measured, or vice versa. In a randomly sampled, continuous population at small spatial scales adhering to a lattice model, the reciprocal of the regression slope of a_r (a measure of genetic differentiation between pairs of individuals, and an estimator of $F_{ST}/(1-F_{ST})$; Rousset 2000), against their geographical distances apart, yields an estimate of neighbourhood size.

Neighbourhood estimates from genetic data are thus fairly tractable. However, in demographic modelling, the two components, density and mobility, often will be of interest. Separating them with precision may be operationally challenging (e.g. for Prickly Forest Skink (*Gnypetoscincus queenslandiae*); Sumner *et al.* 2001). Field-based and genetic estimates of neighbourhood size were both small, with the field-based estimate of 144 individuals falling within the confidence intervals of the genetic estimate (48–184). Mark–recapture data gave a mean dispersal rate of 843 m² per generation, expected to be upwardly biased because the field-based calculations make the unlikely assumption of one-way movement throughout life; the genetic estimate was 404 m² per generation. The field-based density estimate of 13 635 individuals per generation per square kilometre is also expected to be upwardly biased owing to deviations from the underlying model, and compares with the genetic estimate of 6520 individuals per generation per square kilometre. Thus the genetic approaches performed well, and operationally were more tractable than the field-based methods, requiring only a single sampling. Nonetheless, field-based methods are necessary here to estimate density or dispersal if neighbourhood size is to be broken up into its two elements. This can be circumvented if σ is used to develop parameters of dispersal kernels in individual simulations (Broquet and Petit 2009).

Estimating neighbourhood size from a_r has several assumptions (notably small scale, continuous distribution), that will not apply to many organisms. So Rousset and colleagues designed a metric of inter-individual similarity for more mobile organisms, and tested it with simulations and detailed ecological and genetic data from the odonate *Coenagrion mercuriale* (Watts *et al.* 2007). There is close agreement (i.e. within a factor of two) between

estimates of dispersal rate derived using genetic techniques and field methods, and the method is robust to violations of assumptions and applicable in discrete as well as continuous populations. The test statistic of Watts *et al.* (2007) seems appropriate to apply to birds.

An analogous approach to estimating neighbourhood size with very different mechanics draws on the relationship between I and the degree of spatial autocorrelation (measured by Moran's I , very closely related to a probability of descent), between nearest neighbours in a continuous lattice population >30 generations old and for which the population density is not changing rapidly (Epperson 2005). The approach requires only a modest genetic dataset (e.g. >20 alleles among several loci and >100 individuals), and is robust under a very wide range of conditions. Moran's I does not depend on F_{ST} , but rather on biparental inbreeding caused by spatial proximity, and thus should be effective at low levels of genetic structuring. Some of the assumptions of the approach, including spatially and temporally homogeneous densities, could be problematic in many studies. The approach has been criticised on several theoretical and statistical grounds (e.g. Vekemans and Hardy 2004; Rousset 2008).

An entirely different approach can be taken to estimating the history of population size, structure and migration, based on the coalescent (Kingman 1982; Kuhner 2009). The coalescent contains information about population sizes because members of larger ones are on average less related to each other. Coalescent theory relates common ancestry to the size and genetic structure of the population. Estimates of parameters are made from distributions of genealogies using genealogy samplers, yielding good statistical power and robustness even in complicated scenarios (Kuhner 2009). It is increasingly feasible to use multiple genealogies and so estimate uncertainty. Of the core coalescent sampling packages that Kuhner (2009) reviews (BEAST, GENETREE, IM/IMa, LAMARC, MIGRATE) all but BEAST estimate migration rates. They 'vary from slow to excruciatingly slow' (Kuhner 2009), but this can be somewhat ameliorated by running different blocks on more than one computer, and in at least some cases (such as MIGRATE) software is being made appropriate for supercomputing. Other common software that estimates migration rates from genetic data include Arlequin, FSTAT, Genepop, BayesAss+, COLONISE, BATWING, MSVAR and DnaSP (Excoffier and Heckel 2006).

Although coalescent approaches provide the benefit of using all the data rather than summary statistics (Beerli and Felsenstein 2001), the presence of unsampled ('ghost') populations can have a big impact (Slatkin 2005) and are thus, currently, more suitable for systems in which sampling of most population units is tractable. Nonetheless these approaches have been used to good effect in suitable bird systems. Nuclear and mitochondrial sequence markers were applied to the question of population structure and demographic history of the Red-backed Fairy-wren, across the Carpentarian Barrier (Lee and Edwards 2008). Spatial genetics (e.g. using Structure) and coalescent analysis in the program IM under the 'isolation with migration' model of Hey and Nielsen (2004) were conducted. The genetic data strongly support a role 270 000 years ago for onset of cessation of gene flow between the Top End and Cape York across the Carpentarian Barrier (within a subspecies), in contrast to the ongoing movement of two effective migrants per generation between the Eastern

Forest region and Cape York (between subspecies). As well as delimiting potential units for management purposes and quantifying levels of migration among them as an objective and meaningful metric of distinctiveness, work like this can shed light on the impacts of previous climate change and environmental influences, including fire, on biodiversity (Lee and Edwards 2008). The number of good-quality studies in the Australian avifauna is growing (Balakrishnan and Edwards 2009; Joseph and Omland 2009; Pavlacky *et al.* 2009).

Two key programs applied in the kind of study just outlined are IM (and its descendants, IMA and IMA2) and MIGRATE. IM/IMA/IMA2 (Hey and Nielsen 2004) estimate the divergence time between populations, bidirectional migration rates and effective population sizes. IM can estimate population size change as an exponential rate (Kuhner 2009). MIGRATE (Beerli 2006) estimates effective population size and immigration, but assumes that populations are of constant size with dynamics stable for at least $4N$ generations, thus IM/IMA/IMA2 are more relevant for analysis of splitting of young populations (Kuhner 2009). Both programs assume that there are no unsampled populations that input migrants.

Coalescence may register very recent events. A recent study of an Australian forest bird, the Logrunner (*Orthonyx temminckii*), presents an example of using coalescent analyses alongside historical and contemporary landscape data and a typical micro-satellite dataset to quantify the influences historical landscape structure and recent habitat alteration (Pavlacky *et al.* 2009). The paper emphasises the importance of making strong prior predictions, analysing in a statistical environment that can quantify contributions of different factors: in this case, linear mixed models and information-theoretic model selection were applied. It was concluded that contemporary landscape features were approximately twice as influential in explaining genetic structure than was pre-disturbance habitat structure. Coalescent analyses of migration indicated that factors in migration have changed relative importance over time, for example that habitat clearance over the last 100 years (25 generations) has overtaken open eucalypt forest as the most important barrier to Logrunner dispersal. Surprisingly, marginal habitat (tall eucalypt forest) was used extensively for dispersal, whereas movement through high-quality habitat (rainforest) was low. Explanations for these unexpected findings were advanced, including conspecific competition or the inducement for mobile animals to settle if they can, or both (Pavlacky *et al.* 2009). The work is innovative and makes sense biologically, but it seems important to explore the impact of violating key assumptions of MIGRATE (see above; Excoffier and Heckel 2006; Kuhner 2009).

Direct approaches to measuring dispersal. Genotypic approaches offer the ability to identify and enumerate migrants in a sample, for example via assignment tests (as discussed above) and clustering algorithms. Signal resides in the relationships among individual multilocus genotypes and the correlations among alleles from different loci within individuals (i.e. linkage disequilibrium). For many methods (but not all; Peery *et al.* 2008), migrants can be most easily detected in strongly differentiated populations, because when migrants are numerous, residents and migrants become more genotypically similar, making them harder to distinguish (Paetkau *et al.* 2004; Manel *et al.* 2005). Detection of immigrants where all sources are sampled can be

conducted with BayesAss+ and GeneClass2, whereas detection of immigrants from sources that may be inferred is the focus of BAPS, NewHybrids, Structure, Geneland, BATWING, IM/IMA, LAMARC and MSVAR (reviewed and summarised in Excoffier and Heckel 2006). Many birds have large geographical ranges comprising many potential sampling units, and representation of all possible sources is highly unlikely for such species. In such cases, GeneClass2 (Piry *et al.* 2004) may be particularly useful to avoid false positives because it can flag individuals that cannot be assigned to one of the sampled populations, and can test them as not originating in each sampled source.

Relative to indirect genetic methods, direct genetic approaches to estimating dispersal are appealing in that they have few assumptions concerning genetic and demographic equilibria, population models and habitat structure. Unlike indirect approaches, some direct approaches, notably pure assignment tests, do not estimate genetically effective dispersal, but instead yield a point estimate of the movements of bodies within their own lifetimes, which may or may not result in gene flow ('non-effective migration' of Broquet and Petit 2009). Identifying such dispersal can be efficient and useful for practical purposes such as testing movement–connectivity hypotheses, monitoring habitat reconnection and issues of provenance (Abbott *et al.* 2006; Balkenhol and Waits 2009).

Direct genetic methods can be extended to measure effective dispersal by using parentage analysis to assess whether dispersers have subsequently bred (e.g. Hansson *et al.* 2004). This can be applied in continuous populations and does not require genetic divergence among localities, but does require very thorough sampling (Stow and Sunnucks 2004a, 2004b; Cullingham *et al.* 2008; Broquet and Petit 2009). Another approach is to capture the information residing in individuals with immigrant ancestry up to two generations, that is bearing evidence of gene flow. A core tool here under the appropriate sampling regime is BayesAss+ (Wilson and Rannala 2003), a Bayesian method that estimates simultaneously individual migrant ancestries, time since immigration for up to two generations, local inbreeding coefficients and migration rates among pairs of subpopulations. Simulations indicate that BayesAss+ can provide good estimates of migration rates (and their uncertainty) even at quite high levels of migration with modest datasets, as long as genetic differentiation is not too low ($F_{ST} > 0.05$) (Faubet *et al.* 2007). Thus for organisms including many woodland birds that tend to have low F_{ST} , estimates may not be very accurate around the levels of migration at which units transition between demographic dependence and independence (Lowe and Allendorf 2010). This situation is likely to be substantially improved by screening more loci, now quite achievable given technical and informatic advances.

In a similar vein, Bayesian inference of immigration rates (BIMR; Faubet and Gaggiotti 2008), based on a generalised linear model, focuses on the F1 descendants of migrants to estimate genetically effective migration. If migration is very high, the signature of recent migration events will be hard to detect, and simulations suggest that reliable estimates require $F_{ST} > 0.05$ (Faubet and Gaggiotti 2008). Notwithstanding these caveats and limitations, genetic approaches offer new insights and complementary information relative to field-based approaches. They are likely to continue to improve rapidly, and are very effective for some tasks, such as assessing realised mobility between specific

locations, or quantifying immigration and the classes of individual that are the predominant dispersers. Some examples of the sophistication that can be attained from simple genetic datasets follow.

There are many drivers, correlates and impacts of dispersal that have consequences for demography and population persistence, for which genetic tools offer insights (Johnson *et al.* 2009). One important area of research is detailed studies quantifying costs to dispersal. Microsatellite genotyping was used to categorise Great Reed-Warblers (*Acrocephalus arundinaceus*) as philopatric, short- or long-distance immigrants, which was subsequently used as a factor to explain genetically estimated lifetime reproductive success (LRS) (Hansson *et al.* 2004). For males, there were generally fitness advantages of philopatry: survival, mate-attraction, fledgling production and recruitment were all better than for immigrants. Long-distance dispersal was associated with the lowest LRS and survival. For females, the highest local recruitment of offspring went to short-distance immigrants. There was evidence that inbreeding depression was associated with the lower LRS of philopatric females, and the deficit in recruitment for long-distance dispersing females may have resulted from local maladaptation or their offspring being especially prone to long-distance dispersal outside the study area, or a combination of the two. In the Willow Tit (*Poecile montanus*) a similar pattern of low local recruitment in offspring of long-distance dispersing mothers was attributed to greater offspring dispersal rather than a fitness deficit, on the basis that those that recruited locally had normal fitness (Orell *et al.* 1999). Although these studies indicate that gene flow and demographic impacts of long-distance dispersal may be somewhat lower than expected from the number of immigrants, long-distance dispersal remains of critical importance in recolonisation of habitat patches, functioning of meta-populations, and dispersal and gene flow, particularly through systems modified by human impacts (Trakhtenbrot *et al.* 2005). Long-distance dispersal increases when animals must move farther to encounter higher quality habitat, hence dispersal kernels are expected to change in the face of habitat alteration (van Houtan *et al.* 2007; Lowe 2009). Genetic methods are among the most promising tools to characterise dispersal kernels (Dyer 2007).

Three types of genetic connectivity. It is important to recognise different forms of genetic connectivity (Lowe and Allendorf 2010). Classic population genetics theory suggested that rather low amounts of dispersal are required to prevent loss of selectively neutral alleles, and to avoid the harmful effects of inbreeding. Rather surprisingly, the number of migrants, not the proportion, is the critical factor. Heuristically this is because although a single migrant allele has a larger impact on a smaller population, this is counterbalanced by a higher probability of being lost by chance. The estimate that a single immigrant per local population per generation would prevent inbreeding depression and loss of genetic diversity led to the one-migrant-per-generation (OMPG) rule of thumb (Wang 2004). This is quite widely applied in genetic management, and has some empirical and simulation-based support (Wang 2004). The OMPG rule is based on the island population model, and does not account for the fact that N_e is much smaller than N in most species (see 'Fitness genetics', above). Based on simulations, overall, Wang (2004) concludes that if the OMPG rule is interpreted as one genetically

effective migrant per generation, it is a useful and robust approximation, equivalent to an $F_{ST} \sim 0.2$. This level of migration may be termed *inbreeding genetic connectivity* (Lowe and Allendorf 2010). It is a misconception that OMPG is expected to lead to similar allele frequencies among population units: many more than one effective individual per generation are required to achieve near-panmixia, and Lowe and Allendorf arbitrarily define *drift genetic connectivity* as occurring under an order of magnitude more effective dispersal than required to achieve inbreeding connectivity (i.e. $F_{ST} \sim 0.02$ and $N_e m_e \sim 12$). Under this condition, subunits are approximately panmictic. Although the practical significance of drift genetic connectivity may be limited, a third class, *adaptive genetic connectivity*, is critically important. This is the level of genetic influx required to keep useful genes in populations. Because natural selection will promote the retention of useful genetic variation, less migration is required for adaptive genetic connectivity (although natural selection is less effective at smaller effective population sizes and so this ability largely breaks down more in smaller populations; see 'Fitness genetics', above). Depending on the strength of natural selection and the effective population sizes, one migrant in as many as 10 generations will allow the spread of very useful alleles (Lowe and Allendorf 2010).

Given the many assumptions, approximations and known deficiencies of F_{ST} and $N_e m_e$, the rules of thumb above deserve to be treated with much caution. Empirical estimates of the impacts of drift and dispersal on different kinds of genetic variation are challenging, but nonetheless are becoming more common in experimental conservation genetics, and in the wild (Young *et al.* 2000; Sommer 2003; Gilligan *et al.* 2005), including studies of Black Robin (*Petroica traversi*) of the Chatham Islands (Miller and Lambert 2004). Under special circumstances in the field, monitoring of demographic and genetic change may be practical. This has been conducted in birds using direct genetic assignment, which uncovered immigration that would not have been detected using field methods (Keller *et al.* 2001). Within 3 years of an extreme population bottleneck resulting in loss of genetic diversity, the Mandarte Island population of Song Sparrows (*Melospiza melodia*) recovered pre-bottleneck genetic diversity at neutral genetic markers via low levels of immigration from neighbouring populations. The same kind of monitoring could be conducted for candidate genes of ecological importance, many of which are becoming known through genome projects (see 'The genomics revolution and associated technical advances', below). Some studies have made the important next step and investigated the connections among measured dispersal, genetic variation and fitness impacts. For example, among five populations of a butterfly, dispersal was important in maintaining genetic variation, and there were measurable positive individual fitness outcomes of higher mobility and genetic diversity (Vandewoestijne *et al.* 2008).

Estimating effective population sizes

The importance of estimating effective population sizes. The size of a population has a clear negative relationship with proneness to extinction (see 'Fitness genetics', above; Frankham *et al.* 2002), and so estimates of population size are valuable in predicting persistence. Smaller populations tend to have less

genetic variation because loss by genetic drift increases with population size, and retention by natural selection decreases (Frankham 1996). The population size that is most expected to be related to levels of genetic variation is *effective population size*, often denoted N_e . There are many measures of N_e , but broadly it reflects the size of an 'ideal' population (with random mating, equal sex-ratio, equal variance in reproductive success and other assumptions) that has the same level of loss of genetic variation by drift as the population of interest. Because N_e in wildlife is much smaller than the census size, N (Frankham 1995), genetic stochasticity will be important in populations approximately an order of magnitude larger than would otherwise be thought (Frankham 1995; Palstra and Ruzzante 2008). Used for monitoring purposes, downward trends in N_e would usually indicate increased extinction risk (see 'Fitness genetics', above). Gene flow elevates N_e , so population connectivity will generally be beneficial for population persistence (Palstra and Ruzzante 2008). Estimating effective population size with any precision from biological field data is tortuous to the point of impracticality (Frankham 1995), but genetic estimators can perform quite well.

Estimating effective population sizes. Three main kinds of N_e are significant in landscape and wildlife management (Luikart *et al.* 2010). Variance N_e (N_eV) is determined mainly by the number of offspring and temporal change in allele frequencies, and since there are few births in declining populations, this measure is effective in detecting early population declines (Palstra and Ruzzante 2008). In contrast, inbreeding N_e (N_eI) is mostly affected by number of parents and inbred matings, and reflects loss of heterozygosity, which falls with inbreeding, but N_eI does not register a sharp decline until inbreeding accumulates a generation or two after (Allendorf and Luikart 2007, p. 159). In theory, the coalescent effective size (N_eC) reflects all elements of genetic change, but is not currently used much for small populations, in which the assumption of one coalescence per generation is violated (Luikart *et al.* 2010).

Precise N_e estimates are not easy to obtain. For example, to account for overlapping generations, an estimate of N_eV requires comparisons of shifts in allele frequencies between consecutive age-classes, estimates of age-specific rates of reproduction and survival (Jorde and Ryman 1995), and estimates of longer-term N_e need to factor in rates of mutation and recombination (Luikart *et al.* 2010). As long as the assumption of non-overlapping generations does not introduce problematic bias, several methods can perform well with modest datasets (10–20 loci and ~50–60 individuals) (Palstra and Ruzzante 2008; Waples and Do 2008; Wang 2009). One key factor is whether one or more temporal sample is required. In practice, only single samples will usually be available. One promising recent development is a one-sample method based on extracting the signal in various aspects of microsatellite distributions, such as linkage disequilibrium, considered simultaneously in a Bayesian framework (software ONeSAMP; Tallmon *et al.* 2008).

Overall, genetic methods for estimating N_e are more effective than non-genetic ones, are useful for monitoring, comparative and estimation purposes, and are improving rapidly (Palstra and Ruzzante 2008; Luikart *et al.* 2010). They can be applied to track N_e over time, minimally if effective populations are growing or declining. Additional approaches to that question are addressed in the following section.

Estimating population trajectories. Approaches to estimating population trajectories depend on the purpose and data. Demographic expansion or decline is assessed using the following software: BATWING, IM, LAMARC/Migrate, MSVAR, Arlequin and DnaSP (Excoffier and Heckel 2006), with the recent addition of BEAST (Drummond and Rambaut 2007), which uniquely estimates growth models rather than testing for exponential change (Kuhner 2009).

One major distinction is whether the data are based on DNA sequence (often coalescent-based; Kuhner 2009), or based on single-locus, codominant genetic markers such as microsatellites. A second major distinction is whether the estimates are based on population attributes of individual genetic markers such as the mismatch approach applied in Arlequin and various features of microsatellites used in BOTTLENECK (Piry *et al.* 1999) and M-RATIO (Garza and Williamson 2001), or on genotypes of individuals assessed at multiple loci and their relationships, as used in BATWING (Wilson *et al.* 2003) and MSVAR (Beaumont 1999). Methods based on sequences and properties of single loci tend to reflect events further back in time, for example BOTTLENECK registers transient fluctuations in population size at least $0.2N_e$ generations ago, whereas approaches based on individuals estimate very recent population changes, but can be very demanding on data.

Coalescent approaches use DNA-based genealogies, tracking mutational changes along trees, and thus tend to focus on evolutionary timescales (but see example of Australian Log-runner (Pavlacky *et al.* 2009) discussed above, under Indirect genetic approaches to measuring effective dispersal). Although evolutionary timescales (potentially thousands of years) are often perceived as not being relevant to management, they can give important insights into contemporary management issues. For example, the effective population size of an ocean fish, Red Drum (*Sciaenops ocellatus*), was found to be a fraction of 1% of the census size (Turner *et al.* 2002). Coalescent estimates of long-term N_e (using MIGRATE) and a temporal-sampling contemporary method were compared, and it was shown that the very low N_eN was not a recent phenomenon (Turner *et al.* 2002). This was surprising and has important management implications.

Coalescent approaches have been critical in estimation of human-induced demographic change. High-profile examples have used such approaches to estimate the pre-whaling abundance of several species of whale, setting baselines for population recovery, deferring the possibility of resumption of commercial whaling, and enabling the estimation of ecosystem services lost through depletion of whales that cost the lives of millions of seabirds (Roman and Palumbi 2003; Alter *et al.* 2007; Jackson *et al.* 2008). Estimating recent demography from genetic data often uses microsatellites and the coalescent-based method of Storz and Beaumont (2002) in MSVAR, relating it to putative causative factors (e.g. impacts of forest loss on Orang-utans (*Pongo pygmaeus*), Goossens *et al.* 2006; and poaching on African Elephants (*Loxodonta africana*), Okello *et al.* 2008).

Coalescent approaches can also be made directly relevant to management by applying genetic techniques to indicator organisms intimately associated with species of management interest, which as a result of faster rates of evolution are able to generate a useful coalescent signal on short timescales. For example, strong demographic declines and recovery of Cougars (*Puma concolor*)

were not readily quantifiable from Cougar genes, but a fast-evolving feline virus allowed application of coalescent demographic modelling that revealed clear demographic patterns in the Cougars over the last few decades (Biek *et al.* 2006). The estimations were made using BEAST (Drummond and Rambaut 2007), which estimates effective population size, mutation rate and growth patterns for a single population and is particularly useful when temporally separated data are available, because this allows the population size estimator θ to be broken into its even more useful components N_e and mutation rate μ (Kuhner 2009).

How much connectivity is enough? The links between mobility, gene flow and demography

Under the common circumstance that biodiversity and landscape imperatives are traded against economic ones, it would be useful for planning and monitoring to ascertain what level of connectivity in landscapes is sufficient to maintain demographic viability of patch populations and of the entire system. But it is difficult to estimate the level of dispersal at which populations move between demographic dependence and independence (Waples and Gaggiotti 2006; Palsbøll *et al.* 2007; Waples *et al.* 2008). A strong and direct approach to exploring the relationship between mobility and demography is detailed monitoring and field-based quantification, with experimental manipulation. This challenging task has rarely been undertaken, but was conducted on Brown Treecreepers in eucalyptus woodlands, involving translocations of females into different ecological circumstances. Very low female recruitment within fragments and no female dispersal between fragments was observed, and it was concluded that reduced connectivity rather than patch quality was the main driver of demographic decline and patch extinction (Cooper and Walters 2002). The same research program indicated that neither remnant size nor connectivity affected key reproductive parameters, and although females survived worse in smaller remnants, they dispersed readily into small fragments connected to larger areas (Cooper *et al.* 2002b). The overall conclusion was that isolation-sensitivity, not area-sensitivity, was the primary cause of the decline of Brown Treecreepers in the face of habitat fragmentation (Cooper *et al.* 2002b).

At least theoretically, the thresholds for demographically relevant dispersal seem to be high: a rule of thumb based on theory and simulations is that populations become demographically intertwined at dispersal rates above ~10% (Hastings 1993; Waples and Gaggiotti 2006). This leads to the second challenge in estimating how much connectivity is enough for demographic viability: at dispersal rates likely to be high enough to promote demographic connectivity, many genetic estimates of dispersal perform less well. Although there are exceptions, woodland birds are typically good dispersers and managed at large scales, so management units tend to have large N_e and m_e , making them a challenging group. Recent approaches present potential solutions to some of these challenges. Source-sink dynamics may be important in wildlife and especially in landscapes affected by human activity, but information is limited because of the many issues associated with estimating rates of migration among units by field methods, and the limitations of indirect genetic approaches (Peery *et al.* 2008). One largely untapped source of information is the application of parentage assignments to assist

with inferring immigration into candidate sink populations. Peery *et al.* (2008) developed individual-based simulations to model expected distributions of parent–offspring pairs under competing demographic models. These calibrations were used to interpret the observed real-world genetic data, and ascribe relative support for competing demographic models. Encouragingly, unlike most other techniques, the power to differentiate models was *highest* when immigration into sinks was high. The technique suggested that a location supporting threatened Marbled Murrelets (*Brachyramphus marmoratus*) depends demographically on ~2–6% annual immigration from other locations (Peery *et al.* 2008).

Despite what genetics can offer connectivity and demographic modelling, some of it irreplaceable or at least fairly efficient, there are important reasons to integrate field-based information. Notably, capture–mark–recapture (CMR) models are effective for measuring rates of births and deaths as well as mobility, and have improved greatly: multi-state models account for many factors affecting recapture probabilities, contributing to better estimates of demographic parameters of interest (Lowe and Allendorf 2010). In combination with other models, this allows the assessment of the relative importance to population growth of immigration and recruitment (Lowe and Allendorf 2010). However, multi-state CMR modelling requires substantial data collected in precise, repeated regimes.

Demographic projections in real landscapes experiencing environmental change

Ultimately, information about mobility, landscape genetics and demography need to be marshalled into estimates of how populations of organisms will change under different landscape management and climate change scenarios. Population viability analysis (PVA) has been used for decades to estimate population persistence, and now encompasses dynamic biological realism and sensitivity analyses. For example, PVA of the Tasmanian Wedge-tailed Eagle (*Aquila audax fleayi*) was conducted in a spatially explicit fashion using RAMAS Landscape to simulate metapopulation dynamics over time (Bekessy *et al.* 2009). The analysis incorporated high-resolution forest-growth modelling, including fire and other environmental heterogeneity. The main result from a species management perspective was that the ‘No timber harvest’ scenario was the only one tested that resulted in a stable population rather than a declining one, and highlighted the importance of human-induced mortality, particularly of adults.

Detailed biological data were available for Tasmanian Wedge-tailed Eagles, but this will not often be the case in wildlife management. Even extensive datasets can have their limitations, but analyses are increasingly being developed to get the most out of the data. The Common Birds Census was conducted by the British Trust for Ornithology between 1962 and 2001, involving annual censuses of breeding bird populations in ~260 plots per year in which bird territories were mapped. Taking data from six common birds with long time series of up to 20 years, the first 10 or 15 years were used to build models that were used to predict an estimator Population Prediction Interval (PPI) for the remaining 5 years (Saether *et al.* 2009). Critical features that emerged included the importance of modelling density dependence, the magnitude of demographic and environmental stochasticity, and observation error.

Bekessy *et al.* (2009) modelled the Wedge-tailed Eagle population of the Bass District, Tasmania, as a single unit, so data on landscape functional connectivity was not necessary. Modelling landscape structure and functional movements through it present another layer of challenge. This is being met in one predominant way: ‘When the goal is to assess relative consequences of alternative management actions . . . against a background of changing climate and land-use, we see few alternatives to using coupled, spatial simulation models. . .’ (McRae *et al.* 2008). An integrated approach to modelling dynamic factors on wildlife population trends was shown on data from two bird species with different landscape requirements: Winter Wrens (*Troglodytes troglodytes*), typically at high density in mature conifer forests, and Song Sparrows of open, shrubby habitats. Spatially explicit habitat models were developed and applied, along with individual-based vegetation models, overlaid with spatially explicit, individual-based animal population simulations incorporating the effects of habitat factors on survival and dispersal and generating predictions that could be verified in the field. Although simulated landscape-use had large impacts on populations, even small changes in demographic rates resulting from climate change in the scenarios had major impacts on population trajectories. The approach offers the ability combine demography with environmental constraints to explore complex interactions that are otherwise impossible to investigate, yet critical for immediate management decisions.

The success of such approaches will depend on the quality of data. Parameter estimates in real datasets might be subject to very high uncertainty. One response to poor absolute estimates is to rank management actions. Such an approach was applied to a metapopulation of the Glanville Fritillary butterfly (*Melitaea cinxia*) (Drechsler *et al.* 2003). Despite strong data, it was not possible to estimate the extinction risk of the metapopulation with much precision. However, the rank order of management scenarios was very robust to uncertainty. As well as providing guidance on the best management options, the approach can focus research to reduce uncertainty.

Thus it seems that individual-based, spatially explicit modelling offers the best way forward in demographic projections under environmental change. They are readily updated when new data are available, which is a significant benefit for management, where decisions must typically be made immediately but can be adjusted adaptively. To make the most of the algorithms underlying such approaches and to integrate with landscape, environment, climate and socioeconomic information, the best way forward is spatio-temporal dynamic models that simulate mate-selection, genetic exchange, dispersal, and mortality as probabilistic functions of landscape and environmental characteristics (Strand and Niehaus 2007; Balkenhol *et al.* 2009a). Recent software development in this field has increased processing speed thousands of times (Allen and Dytham 2009). Developments in this area were highlighted in Balkenhol *et al.* (2009a), who noted in particular CDPOP (Landguth and Cushman 2010), and BIOMAPPER (in the EcoGenetics suite <http://www2.unil.ch/biomapper/ecogenetics/index.html>, accessed 13 September 2010). These interface extremely well with the kinds of data and approaches that are used in field-based and molecular population biology research on organisms in landscapes affected by human activity.

The genomics revolution and associated technical advance

In the past, development of molecular markers and the cost of screening were sometimes a bottleneck in the application of genetic approaches to landscape and wildlife management. Both problems were largely removed with incremental advances and efficiencies but have recently been addressed decisively by next-generation sequencing and genomics (Vernesi and Bruford 2009). Microsatellite development can now be achieved rapidly for very little work and \$US1000–2000 using next-generation sequencing, and costs will continue to fall (Abdelkrim *et al.* 2009). It is also tractable to apply the same or equivalent markers among species and obtain quantitatively comparable estimates of population demography, for example using resources based on comparing the Chicken genome with genomes of other birds including the Zebra Finch (Hillier *et al.* 2004; Backström *et al.* 2008; Karaiskou *et al.* 2008; Kimball *et al.* 2009). These have made available many hundreds of coding exons, non-coding introns and untranslated regions, for application to any bird. Data on the evolutionary behaviour and information content of such markers is growing rapidly and yielding estimates of substitution rates for application to comparative demographic modelling (Lee and Edwards 2008; Balakrishnan and Edwards 2009). Some of the patterns being uncovered for birds are unexpected. For example, anonymous loci of Red-backed Fairy-wrens have approximately an order of magnitude more diversity than loci in the non-coding regions of the human genome, and much higher than in bird introns (Lee and Edwards 2008). Overall, bird genomes seem to be fairly stable over very long evolutionary periods, making comparisons among species reasonably powerful (Backström *et al.* 2008). One difference, compared with most vertebrates, is that female birds are heterogametic (have two different sex-chromosomes, ZW), whereas males are homogametic (ZZ). Unlike mammals then, the sex-limited chromosome, W, is in females, and its patterns should be correlated with those of the maternally inherited mitochondrial DNA (Hellborg and Ellegren 2004).

Given global environmental change in climate and habitat, a major challenge for landscape genetics is to understand the distribution and future of adaptive variation (Johnson *et al.* 2009). Technology and analyses are advancing extremely rapidly, making tractable the identification of ecologically significant genes and the ability to screen them in many individuals across landscapes (Wilding *et al.* 2001; Joost *et al.* 2007; Vernesi and Bruford 2009). It should be possible to apply these approaches to project persistence of organisms under changing environments, and also in biomonitoring (Hoffmann and Daborn 2007).

Some very exciting examples of functional genomics in landscapes are already beginning to emerge in the literature on non-model organisms. The dopamine receptor D4 gene (DRD4) has been of interest for some years owing to its role in novelty seeking or exploratory behaviour in animals and is one of the most profound ‘personality genes’ known in humans, and a single-nucleotide DNA polymorphism in DRD4 predicts some of the variation in exploratory behaviour of Great Tits (Korsten *et al.* 2010). These kinds of developments underpin the genetic basis of behaviour relevant to dispersal, consistent with suggestions that long-distance dispersal seems heritable (Orell *et al.* 1999; Hansson *et al.* 2004). The potential for human impacts to radically

alter the distribution of such genes is considerable and could have substantial demographic impacts. An extensive research program of the relationship between ‘personality’ and demography in fish has uncovered physiological mechanisms linking climate change, metabolism, behaviour and mortality in lake-sized experiments (e.g. Biro *et al.* 2007). ‘Conservation genomics’ has the potential to offer profound insights into dispersal and persistence in metapopulations via functional genes underpinning dispersal, reproductive ability, and thermal biology (e.g. in California Condor (*Gymnogyps californianus*); Primmer 2009).

Finding candidate genes for important traits with spatial and demographic consequences is already underway, including extensive genomics research in Zebra Finches (Clayton 2004). Such resources are transferable to many other species: DNA of Common Whitethroat (*Sylvia communis*) hybridises usefully to the Affymetrix Lund-zf array designed for Zebra Finch, from which the Common Whitethroat diverged 25–50 million years ago (Naurin *et al.* 2008). The ability of these approaches to find genes of interest is virtually unlimited, and examples to date include key avian traits such as vocal learning and colouration (Axelsson *et al.* 2008).

Comparative genomics can find genes bearing signals of adaptive evolution, which are disproportionately more common for critical functions (Axelsson *et al.* 2008). Major Histocompatibility Complex (MHC) class I and class II genes are keys to fitness, conferring protection against serious disease. For example, in Great Reed-Warblers, protection from avian malaria parasites *Haemoproteus payevskyi* and *Plasmodium* spp. was provided by MHC class I diversity and particular alleles (Westerdahl *et al.* 2005). Rates of infection can be very high: infections were detected by genetic approaches in 69 of 105 species of Australian and Papuan birds, and 44% of 428 individuals surveyed, with substantial variation among host families (Beadell *et al.* 2004). *Haemoproteus* are more host-specific than *Plasmodium*, suggesting that *Plasmodium* pose the greater threat of passing into new species owing to human-induced environmental variation. Although MHC is important in disease-resistance, it is increasingly implicated in other functional systems, including mate-choice, song and colouration. Female Savannah Sparrows (*Passerculus sandwichensis*), mate non-randomly with respect to MHC variation in males, consistent with females seeking immune system diversity for their offspring (Freeman-Gallant *et al.* 2003).

Critically important genes such as those noted above suggest a role for molecular approaches in monitoring the impacts that environmental changes have on organisms (Hoffmann and Daborn 2007). This has great potential to provide early warnings because the genetic make-up of populations is usually altered well before populations become extinct.

Contributions of landscape and dispersal genetics to economic levers for management

In a survey of the application of science in landscape and wildlife management, only ~11% of management decisions drew on scientific reviews, and 2.4% on primary literature (Sutherland *et al.* 2004). The reasons given were that applying science is too time-consuming (65%) and too hard to understand (25%). This situation could be improved by integrating science into the major

decision-support environments of the management agencies. Estimates of population structure and connectivity, including specifically drawing on molecular population biology, have been incorporated into economic levers for biodiversity benefit (Balkenhol *et al.* 2009a; Hartig and Drechsler 2009). In recent developments linking effective dispersal of wildlife to market-based incentives in complex landscapes, genetic measures of connectivity and dispersal are used as the metric to ascribe credits to different proposed actions in the landscape (Bruggeman *et al.* 2009). Neutral markers and functional genes could be used to test the success of these approaches.

Genetic studies need samples

The approaches outlined in this article require that samples be obtained from individual organisms and connected as far as possible to basic information such as date, location, species, sex and so on. Demographic estimation is generally greatly facilitated by temporal samples and, of course, by geographical and life-stage sampling, and raw numbers. Sample collection does not have to be complicated, expensive or time-consuming, and can be as simple as putting a feather into a paper envelope or cutting the end of the shaft into a tube of Chelex (Sloane *et al.* 2000), although the effectiveness of such very simple approaches depends on the situation and questions to be answered. Avian red blood cells are nucleated, so blood is a much richer source of DNA than for many vertebrates. Nonetheless, it is common for significant investments of time, resources and inconvenience to birds (e.g. being mist-netted) to be undertaken without collection of samples for DNA analysis, hence the plea of DeYoung and Honeycutt (2005):

At the very least, wildlife professionals should consider the collection and archiving of tissue samples for future analyses.

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