1 **Genetic and genomic monitoring with minimally invasive sampling methods**

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Abstract

Emerging genomic technologies are reshaping the field of molecular ecology. However, many modern genomic approaches (e.g., RAD-seq) require large amounts of high quality template DNA. This poses a problem for an active branch of conservation biology: genetic monitoring using minimally invasive sampling (MIS) methods. Without handling or even observing an animal, MIS methods (e.g. collection of hair, skin, faeces) can provide genetic information on individuals or populations. Such samples typically yield low quality and/or quantities of DNA, restricting the type of molecular methods that can be used. Despite this limitation, genetic monitoring using MIS is an effective tool for estimating population demographic parameters and monitoring genetic diversity in natural populations. Genetic monitoring is likely to become more important in the future as many natural populations are undergoing anthropogenically-driven declines, which are unlikely to abate without intensive management efforts that often include MIS approaches. Here we profile the expanding suite of genomic methods and platforms compatible with producing genotypes from MIS, considering factors such as development costs and error rates. We evaluate how powerful new approaches will enhance our ability to investigate questions typically answered using genetic monitoring, such as estimating abundance, genetic structure and relatedness. As the field is in a period of unusually rapid transition, we also highlight the importance of legacy datasets and recommend how to address the challenges of moving between traditional and next generation genetic monitoring platforms. Finally, we consider how genetic monitoring could move beyond genotypes in the future. For example, assessing microbiomes or epigenetic markers could provide a greater understanding of the relationship between individuals and their environment.

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INTRODUCTION

The current era of rapid global environmental change (Zalasiewicz et al., 2011) is predicted to lead to a rapid loss of biodiversity (Pimm et al., 2014). To assess and mitigate the impact of this loss, many national and international organizations have established biodiversity monitoring strategies (e.g., Kurtz et al., 2001; United Nations Environment Programme Convention on Biological Diversity SBSTTA, 2003). Key tools for biodiversity monitoring utilise methodological approaches from the field of genetic monitoring, relying on genetic tools for evaluating change (Stetz et al., 2011). Genetic monitoring focuses on quantifying temporal changes in population genetic metrics, or other population data, generated using molecular markers. Genetic monitoring can be used to estimate many biological parameters of interest, which have previously been classified as follows: Category I - demographic parameters such as abundance, vital rates, occupancy, hybridization, disease status; Category II - population genetic parameters including genetic diversity, structure and effective population size; and Category III - evolutionary adaptation to exploitation or climate change (Schwartz et al., 2007; Stetz, 2011). Here, we examine genetic monitoring approaches that use noninvasive (e.g., naturally shed feathers) or minimally invasive (e.g., buccal swabs) samples (hereafter MIS) because wildlife ecology and conservation has benefitted greatly from the new data provided by these approaches (Beja-Pereira et al., 2009).

Genetic monitoring using MIS approaches was first introduced in 1992 as a method to obtain genetic samples from brown bears (*Ursus arctos;* Höss et al., 1992; Taberlet & Bouvet, 1992, see Box 1) and to study social structure in chimpanzees (*Pan troglodytes;* Morin & Woodruff, 1992). MIS has become the method of choice for genetic monitoring of many vertebrate species because genetic sampling of hair, feces, biopsies or feathers provides DNA from free-ranging animals that can be used to identify individuals in time and space and generates genetic data without having to catch, handle or in some cases, even observe them

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(Beja-Pereira et al., 2009; Schwartz et al., 2007; Waits & Paetkau, 2005). In the last 25 years, researchers have demonstrated a variety of important applications of MIS including detecting rare species (Palomares et al., 2002; Valière et al., 2003), estimating population size and other demographic parameters (Carroll et al., 2013; Kendall et al., 2009; M. H. Kohn et al., 1999; Rudnick et al., 2005; Woodruff et al., 2016; Woods et al., 1999), evaluating genetic diversity and gene flow (Epps et al., 2005; Gerloff et al., 1999; Lucchini et al., 2002; Palsbøll et al., 1997), detecting movement and migration (Dixon et al., 2006; Proctor et al., 2005), evaluating social structure (Constable et al., 2001; Ford et al., 2011; Morin et al., 1994), detecting hybridization (Adams et al., 2003; Bohling et al., 2016; Steyer et al., 2016), monitoring disease epizootics (M. H. Kohn & Wayne, 1997; Schunck et al., 1995), identifying diet items (De Barba et al., 2016; Höss, 1992; Taberlet & Fumagalli, 1996), and wildlife forensic applications (Banks et al., 2003; Ernest et al., 2002; Lukoshek et al., 2009; Wasser et al., 2004).

There is now a wealth of published evidence that MIS is more cost-effective than traditional methods that require other technological approaches (e.g., camera trapping, tracks and signs and even trapping animals) and that collection and analysis of larger sample sizes are often possible (De Barba et al., 2010; Marucco et al., 2009; Solberg et al., 2006; Stenglein et al., 2010), prompting many wildlife managers to shift to MIS approaches. Extensive methodological and analytical development has been invested in establishing protocols to maximize success rates and minimize error rates when using these low-quality DNA sources for genetic monitoring (Beja-Pereira et al., 2009; Broquet & Petit, 2004; Miquel et al., 2006; Morin et al., 2010; Smith & Wang, 2014; Taberlet, Griffin, et al., 1996; Taberlet & Luikart, 1999; Waits, 2005; Wang, 2016). Genetic monitoring is set to become more important in the future, largely because many vertebrate species have undergone rapid, anthropogenic population declines (Li et al., 2016) that are unlikely to abate without intensive management

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efforts. Fortunately, the genomic revolution of the early 2000s has given rise to a variety of more precise or more powerful molecular techniques that will make genetic monitoring even more effective in the future.

New technologies for genetic monitoring typically rely upon single nucleotide polymorphisms, or SNPs (Morin et al., 2004). Unlike more conventional DNA markers such as microsatellites, SNPs have relatively few alleles per locus (theoretically up to four but usually only two due to mutation/drift equilibrium; Glaubitz et al., 2003). The advantages of SNP loci are thus not in their allelic diversity, but in a) the number of loci than can be surveyed simultaneously and b) the relative ease of scoring, analysis and modeling of SNP genotype data due to the digital/binary nature of the data. The latter point contrasts favourably with the near continuous distribution of microsatellite alleles that can be difficult to consistently characterize due to scoring errors. One major disadvantage of SNP markers is that they have more limited application across species than microsatellite markers and are often species-specific. In addition, they are more prone to ascertainment bias, as they are selected because of their high polymorphism in the populations of interest but are often monomorphic in even closely related populations (Gautier et al., 2009). However, SNP-based approaches have great potential for noninvasive genotyping and will be the focus of this review.

SAMPLING AND METHODOLOGICAL CONSIDERATIONS

Sampling Issues

Sampling strategies for non-invasive material in the natural environment can be carried out randomly, opportunistically, or using standardized designs. When planning a non-invasive sampling strategy, it is important to account for patterns of social structure (random or nonrandom association of individuals), habitat-use, and availability of the material produced

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(feces, urine, partially consumed food). This is, in part, because it is important to maximize sampling opportunities for elusive species, given the labor-intensive nature of field work, but also because certain parameters (e.g., genotype capture-recapture methods to estimate census size) require the application of assumptions about sampling that may or may not be satisfied if sampling is conducted incorrectly. It is also important to consider the temporal sampling interval which can affect sample sizes, genotyping success rates, genotyping error rates and impact the ability to meet modeling assumptions for mark-recapture and occupancy analyses (Lonsinger et al., 2015; Woodruff et al., 2015).

Sampling strategies may be designed to maximize the total number of individuals detected (typically used for minimum census estimates and population genetic studies) or to maximize recaptures using high intensity sampling over a limited geographic range (to estimate ranging behavior or territory size for an individual or group of individuals, and estimate population size e.g., Rudnick et al., 2008). For many population genetic parameters (category II monitoring in Schwartz et al., 2007) sampling should be designed to be random with respect to kin (this can also be addressed by *post hoc* data pruning, but see Waples & Anderson, 2017).

Molecular Methodologies

The human and agricultural genetics communities have already embraced SNPs for genotyping because of their myriad advantages over microsatellites (FAO Commission on Genetic Resources for Food and Agriculture Assessments, 2015). There are many methods for genotyping thousands of SNPs, including variations on RAD-seq (Baird et al., 2008) and genotyping-by-sequencing (Elshire et al., 2011). These approaches could be useful in MIS if sufficient DNA can be obtained (e.g., Chiou & Bergey, 2015), but these anonymous-marker approaches often require considerably more DNA than is typically available to biologists

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using MIS. Furthermore, they genotype far more loci than needed for individual identification and assessments of relatedness, population structure, and other parameters of general interest in genetic monitoring studies and are thus economically inefficient. However, some next generation sequencing and advanced genotyping methods are particularly suitable for the low quality or quantity of DNA that are typically obtained from MIS; we broadly categorise these into SNP arrays and target enrichment methods.

SNP arrays

Platforms that more efficiently assess relevant numbers of SNPs include the Fluidigm SNPtype assay (Table 1, 2). The fisheries community has embraced SNP genotyping assaying scores of loci with the Fluidigm platform (Bonanomi et al., 2016; Campbell & Narum, 2011; Hauser et al., 2011) and recently, several wildlife studies have also used this platform in a monitoring context (Table 1: Doyle et al., 2016; Kraus et al., 2015; Nussberger et al., 2014). The Fluidigm SNP type assay seems to have relatively low error rates (e.g., 0.2% in DeWoody et al., 2017; 0.4% in Doyle, 2016; 1-3% in Kraus, 2015; 1.7% in Nussberger, 2014). The low error rate is important for all aspects of molecular ecology, but particularly for inferences of individual identification, parentage, and relatedness.

A technologically similar platform, Amplifluor SNP genotyping system, has been shown to be highly sensitive with low quality/quantity samples: there was a high level of genotyping success with as few as 10 DNA templates per assay (Morin & Mccarthy, 2007). Mesnick et al., (2011) used 8 microsatellite loci and 38 Amplifluor SNP loci to investigate the population structure of North Pacific sperm whales (*Physter macrocephalus*). The Amplifluor SNP loci had a similar error rate (1.4%) to the microsatellite loci (0.9%) in this study (Tables 1 and 2).

In contrast to the fluorescence-based platforms, the MassARRAY platform uses mass spectrometry to determine SNP alleles. The platform has potential for MIS samples: in a

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recent study, the MassARRAY system successfully genotyped a higher proportion of puma scat samples (59.8%) than a conventional microsatellite genotyping approach (39.9%), with no significant difference in error rates between the methods (Fitak et al., 2015). However, another study that used both microsatellite genotyping and MassARRAY assays to genotype Bornean elephant blood and faeces found a lower rate of genotyping success and higher error rates for the SNP platform in faecal samples (Goossens et al., 2016). The authors found a trade off between genotyping success and multiplexing level, with smaller multiplexes having greater success (Table 1, Goossens et al., 2016), and suggested that the issue could be the lower quality of faecal DNA.

Target enrichment methods

The aim of target enrichment is to selectively capture genomic regions of interest before high throughput sequencing. Target enrichment methods can be a highly sensitive way of selectively and reproducibly obtaining genomic data. Genomic regions can be selectively targeted using PCR, as well as in-solution or array-based methods. PCR-based methods are suitable for MIS as they typically require only small amounts of starting material and, by utilising multiplex PCR and combinatorial barcoding techniques, can be cost-effective. One such method is GT-seq (Campbell et al., 2015, Table 2), which has been used to genotype steelhead trout (*Oncorhynchus mykiss*) to assess abundance, migration timing and stock composition (Hess et al., 2016; Matala et al., 2016). GT-seq also appears to have a low error rate; the method had a 99.9% concordance rate with genotypes generated with the Fluidigm platform. The method may require additional optimisation for low quality/quantity DNA samples, although it works well with sheared DNA templates, success rates drop off when DNA concentrations <10 ng/uL (N. Campbell, pers. comm.).

Another targeted PCR approach has focused on the use of high-throughput sequencing to generate microsatellite genotypes (e.g., De Barba et al., 2016). This approach could have

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the advantage of linking into legacy datasets if the same sets of loci can be used in the new and traditional microsatellite genotyping platforms. It also has the benefit of rapidly generating consensus genotypes using bioinformatic analysis pipelines. However, optimisation and validation steps are required to move microsatellite genotyping on to a new sequencing platform (De Barba et al., 2016).

DNA capture methods, in conjunction with high throughput sequencing, have been used to investigate phylogenetic questions (e.g., Hancock-Hanser et al., 2013), but the application of such methods to within-population studies has been limited thus far. One successful example was the use of custom biotin-tagged RNA baits to capture genomic DNA from fecal samples from 62 wild baboons (*Papio papio*). The enriched libraries were sequenced with Illumina HiSeq and provided sufficient genomic markers to undertake pedigree reconstruction (Snyder-Mackler et al., 2016). Another study, using bait captures generated from the Agilent SureSelect system, successfully sequenced more than 1.5 Mb of nuclear DNA and the entire mitochondrial genome from chimpanzee feces (Perry et al., 2010). These studies highlight the potential of bait capture approaches, both custom and using a commercial provider, in a genetic monitoring context. Such approaches could be aided by the use of novel extraction methods that enrich samples for endogenous DNA, such as FaecalSeq (Chiou & Bergey, 2015).

Data Analysis

SNP array platforms have proprietary software packages that are used to score genotypes and often provide a degree of confidence in genotype calls (e.g., Sequenom platform). Such automated calling is not always accurate, and it is recommended that researchers visually check the data for error. Target capture approaches that use high throughput sequencing tend to have custom bioinformatics pipelines (e.g., Campbell et al., 2015). However, the major

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steps are similar between studies and include filtering of reads based on quality scores and demultiplexing reads into samples and loci. Genotyping is then conducted using custom bioinformatics tools and information such as the relative frequency and read depths of sequences likely to be alleles versus sequencing artifacts (Campbell et al., 2015; De Barba et al., 2013).

Quality Control

Genotype data are imperfect and subject to missing genotypes (errors of omission) as well as erroneous genotypes (errors of commission; Faria et al., 2011). Missing and erroneous genotypes can be due to many possible causes, such as suboptimal genotyping protocols, limited DNA quantity and quality, contamination, and human error (Bonin et al., 2004; Pompanon et al., 2005). MIS data are especially problematic due to the low DNA quality and quantity, and can incur a high rate of missing and erroneous genotypes. Markers themselves are also imperfect. Loci can have null alleles which produce no observable phenotypes (Dakin & Avise, 2004) and thus null allele homozygotes would be scored as missing data, whereas a null allele heterozygote would be scored (erroneously) as a homozygote of the observable allele.

Missing and erroneous genotypes affect many genetic analyses, yielding potentially biased and imprecise results and, in turn, incorrect conclusions. Broadly speaking, analyses that use genotype data are more severely impacted than analyses that use allele frequency data. For example, genetic differentiation, measured by F_{ST} (Wright, 1931) and evaluated by several estimators (Nei, 1973; Weir & Cockerham, 1984), is determined by marker allele frequencies. Since missing and erroneous genotypes do not substantively change allele frequencies, such errors tend to have small effects on F_{ST}. In contrast, genotype based analyses, such as inferences of identity, relatedness and relationship, are strongly influenced

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by data quality. Ignoring or underestimating genotyping errors can lead to false parentage exclusions (Dakin, 2004; Wang, 2010), false sibship exclusions (Wang, 2004), false exclusion of duplicated individuals and thus overestimation of population size (Creel et al., 2003; Waits & Leberg, 2000).

The impact of missing and erroneous genotypes also depends on how they are distributed among loci and among individuals. The best scenario is a uniform distribution, such that no specific loci and no specific individuals are too problematic to be useful. However, with MIS samples, missing and erroneous genotypes are usually clustered among individuals because the sample DNA quality and quantity can differ substantially among samples, and error rates have been shown to vary considerably across loci (Broquet, 2004; Campbell, 2015; Gagneux et al., 1997; Paetkau, 2003).

A source of error common to both microsatellites and SNP genotypes from next generation sequencing (NGS) platforms is allelic dropout (Gagneux et al., 1997). This is where heterozygous genotypes inferred from sequence data may be incorrectly typed as a homozygote. Allelic dropout is generally caused by random effects that result in missing one of the two alleles at a diploid locus, it is also correlated with lower coverage (5-20x; R. Nielsen et al., 2011). If the underlying genotype is a heterozygote, then this type of error would lead to one of the two possible homozygous genotypes at a similar probability. Traditionally, a single best genotype is reported for an individual at a locus. The large uncertainties of such called SNP genotypes mean that erroneous results could be produced, such as an overestimation of inbreeding (Vieira et al., 2013) and biased estimates of relatedness (Vieira et al., 2016).

The best practice now is to call all possible genotypes at a SNP locus with corresponding likelihoods that summarize the quality and evidence of the reads data, as well as incorporating information on population-level allele frequencies (Nielsen et al., 2011). By

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using genotype likelihoods to account for uncertainties at individual genotype level, an appropriately designed program can yield unbiased and accurate estimates of parameters such as inbreeding and relatedness (Vieira et al., 2013, 2016), even when the average coverage is very low and thus the genotype data are highly uncertain (Buerkle & Gompert, 2013). Buerkle & Gompert (2013) show that partitioning the sequencing effort maximally among individuals and obtaining approximately one read per locus and individual (1X coverage) yields the most information about a population. More statistical methods urgently need to be adapted or developed to take advantage of genotype likelihoods. One obstacle is computational burden, which increases enormously by considering three possible rather than a single genotype at each locus for each individual, though increasingly sophisticated algorithms and parallelization may mitigate this issue.

The fundamental strategy for improving data quality is by enhancing DNA quantity and quality, reducing contamination, improving PCR protocols (or NGS coverage), and other technical improvements (Bonin, 2004; Paetkau, 2003; Pompanon, 2005). As with microsatellite genotyping (Bonin, 2004), the best practice is to report error rates from SNP genotype studies. There are two categories of mistyping rate estimation. One category is based on duplicated genotype data (i.e. an individual is genotyped independently multiple times at a locus), measuring actually the consistency of repeated genotypes (e.g., Broquet et al., 2004) or estimating the error rates of repeated genotypes (e.g., Johnson & Haydon, 2007, Zhan et al., 2010). These methods generally overestimate the mistyping rate of the final genotype dataset, because repeated genotyping allows for the detection and elimination of such errors in the final consensus genotypes. This has been a common method for reporting genotype error rates in many SNP array studies (Table 2).

The second category for estimating mistyping rates is based on the final consensus genotypes, and is accomplished by examining the genotype against either the Hardy-

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Weinberg equilibrium (e.g., Hosking et al., 2004) or the Mendelian segregation law in a known (e.g, Sobel et al., 2002) or reconstructed pedigree (e.g., Wang & Santure, 2009). The former is effective only in detecting null alleles and allelic dropouts that can cause directional deviations from Hardy-Weinberg proportions (i.e. an excess of homozygotes), but is ineffective for mistypings that do not cause detectable distortions, such as false alleles. This error estimation approach can have low power (e.g., Cox et al., 2006), and relies on the absence of confounding factors, such as strong selection, inbreeding and population structure. Some methods have been developed to make joint estimates of null allele frequencies and inbreeding (e.g., Hall et al., 2012). How well such methods work has not been thoroughly evaluated, however.

Pedigree, either known or inferred, can be used in likelihood methods to detect erroneous genotypes and to estimate mistyping rate at each locus (Sobel et al., 2002; Wang, 2009). These methods can be used to infer null allele rates, allelic dropout rates, and false allele rates, and are highly robust to the violations of some common assumptions such as random mating and the absence of inbreeding population structure. Such mistyping estimation methods, together with data missing rates, measure data quality. More importantly, these methods allow downstream analyses to effectively filter out the noises in exacting information from the genotype data and in arriving at robust and accurate analysis results (e.g., Kalinowski et al., 2007; Wang, 2004).

QUESTIONS AND METRICS

Category IA: Individual identification and its application

Abundance/density

The recapture of individuals, identified by their genotype, across time and space has allowed genetic monitoring to become a key tool in estimating abundance, density, and demographic

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parameters in a variety of species. It has been particularly important in species that are evasive, endangered (Taberlet et al., 1997), dangerous (Stenglein et al., 2010) or otherwise difficult to capture/recapture (Constantine et al., 2012), such as those that show limited variation in natural markings, reducing the usefulness of conventional identification from photographs (e.g. juvenile cetaceans, Carroll et al., (2016)). Using genetic monitoring to estimate abundance spans methods from the enumeration of the number of genotypes in a region (Taberlet et al., 1997), to single-session models (Miller et al., 2005; Petit & Valière, 2006), to occupancy (Lonsinger et al., 2017; Marucco et al., 2012), to complex mark recapture models that integrate sex, age and reproductive status information (Carroll et al., 2013; Woodruff et al., 2016). The advent of spatial mark recapture models (Efford et al., 2004, 2011; Royle & Young, 2008) has greatly improved analytical tools for density estimates using genetic monitoring approaches (Mollet et al., 2015; Russell et al., 2012; Thompson et al., 2012).

Population estimation in genetic monitoring has relied on individual identification using microsatellite loci to date. Recognition that genotyping error, correlated with low quality DNA templates, can create large biases in population abundance estimates (Waits & Leberg, 2000) has required the development of methods that generate consensus genotypes from multiple PCR replicates (Taberlet et al., 1997) or models that directly incorporate genotyping error (Lukacs & Burnham, 2005). In transitioning to the genomics era, new approaches such as direct sequencing of microsatellite loci (De Barba et al., 2016) and SNP analysis will be used (Fitak et al., 2015; Kraus et al., 2015). Large panels of markers from next-generation sequencing will allow for the more efficient identification of related individuals. This will allow the use of close kin mark recapture models, which extend the idea of using the recapture of individuals to the recapture of close kin to estimate demographic parameters such as effective population size (Wang, 2009; Bravington et al. 2016).

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Demographic parameters

Effective management of populations and species requires sound knowledge of key demographic parameters, such as survival and growth rates. The most common way to estimate such parameters is from long-term studies that follow individuals over time (McClintock et al., 2009). Long-term MIS studies have been an effective way to estimate survival and growth rates in a range of species, by tracking individuals using their genotype. This has been accomplished using mark recapture models in species such as southern right whales (*Eubalaena australis*; Carroll et al., 2013, 2016), the dendrobatid frogs (*Allobates femoralis*; Ringler et al., 2015), Māui dolphins (*Cephalorhynchus hectori maui*; Baker et al., 2013) and imperial eagles (*Aquila heliaca*; Rudnick et al., 2005). The definitive DNA marks provided by genetic monitoring can provide robust population estimates in age-structured populations that can be difficult to observe in the wild. The difference between observational and MIS genetic population estimates can have profound impacts on demographic models and associated conservation actions (Katzner et al., 2011).

Individual space use and movement

Genetic monitoring using MIS can also provide valuable information on individual space use, movement patterns and dispersal. This approach has been used to monitor population expansion and individual dispersal distances in reintroduction efforts for brown bears (De Barba et al., 2010), gray wolves (*Canis lupus*; Stenglein et al., 2010), and Columbia Basin pygmy rabbits (*Brachylagus idahoensis*; Demay et al., 2017), investigate connectivity between migratory habitats in humpback whales (*Megaptera novaeangliae*; Constantine et al., 2014; Garrigue et al., 2011), to monitor roosting movements in eagles (Rudnick et al., 2008) and to detect natural range expansion (Carroll et al., 2014; Valière & Petit, 2003) using microsatellites. MIS using microsatellites has also been valuable for assessing the effectiveness of corridors (Dixon et al., 2006) and evaluating potential barriers (Epps et al.,

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2005; Kendall et al., 2009; Proctor et al., 2005). More recently, SNPs have been utilized to estimate pedigree-based dispersal models in brown bears (Norman et al., 2015) and to infer individual provenance (i.e., identify potential migrants) based on the distribution of pairwise relatedness (DeWoody et al., 2017).

Relatedness and kin structure (kinship)

Since the development of relatively large panels of markers (microsatellites and more recently SNPs), those panels have been used to monitor the existing relationships between individuals of a given population, either to investigate genetic and social structure, gene flow, reconstruct pedigrees or minimize inbreeding (Caniglia et al., 2014; Da Silva et al., 2010; Jones et al., 2002; Peters et al., 1999; Stenglein et al., 2011). Metrics generally used to measure relatedness between two individuals estimate either a summary statistic (such as coancestry coefficient it its equivalents), which would correspond to the relatedness between two individuals, or the probability that two individuals are linked with a particular relationship (parent-offspring, first cousins, self-outbred sibs…) given the data (Wang, 2011). In some cases, the reliability of relatedness estimates can be limited, especially when the population under study exhibits low genetic variation for the marker set; therefore *a priori* simulations should be performed to select the most appropriate estimator and assess its accuracy (Glaubitz et al. 2003; Taylor, 2015). The development of NGS tools is expected to increase the availability of high density panels, thus improving the reliability of estimators. It may also allow the use of new metrics, such as, for instance, segment-based ones, considering the measurement of coancestries based on shared segments of identify by descent, instead of averaging, marker by marker, the probability that two alleles are identical at state (De Cara et al., 2013).

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Category Ib: Defining species or conservation units

Occupancy and range

Species and site occupancy and presence/absence analysis relies on quantifying detection rates and especially understanding whether a target species is present, but undetected; information needed to avoid biased estimates of site occupancy, colonization, and local extinction probabilities (e.g., MacKenzie et al., 2003). Molecular data can augment these studies, enabling more accurate detection even at very low levels of occupancy using environmental samples and DNA barcoding (e.g., Boothroyd et al., 2016) or faecal samples of uncertain species identity (e.g., Faria et al., 2011; Palomares et al., 2002; Stanton et al., 2016), although its use is again severely constrained by DNA quality considerations. For example, Stanton et al., (2016) assayed faecal samples from an unsurveyed region in the Democratic Republic of Congo for the presence of okapi (*Okapia johnstoni*). Of the 24 fecal samples detected, only 12 yielded DNA but of these six were identified as okapi and these yielded four mitochondrial haplotypes (hence allowing the inference of minimally four individuals being present). Advances in environmental DNA (eDNA) analysis are enhancing our ability to examine past and present occupancy and range of various species (see Box 2).

Social and genetic structure

In addition to the presence/absence and censusing of individuals, additional information can be gained from MIS studies on the socio-genetic structure of the population being surveyed. This has become a necessity in certain fields (especially in primatology) where, even if individuals can be observed and identified, invasive sampling is regarded as unethical and is often prohibited. Such studies may allow identification of social group-mediated genetic structure and inferences on sex-biased dispersal and how these may be modified by habitat fragmentation (e.g., Minhos et al., 2016) and/or hunting and exploitation (e.g., Ferreira da Silva et al., 2014). Understanding social structure and spatial assortment of related individuals

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using MIS is also an important factor underpinning the accuracy of capture-recapture molecular censusing (Miller, 2005; Zhan et al., 2006).

Both in socially structured and unstructured species, population boundaries may spatially coincide with a sampling area being studied using MIS methods. In such cases, it is important to know where these boundaries lie in order to infer the underlying demographic processes structuring the population(s), and to assign individuals to those populations using the correct allele frequency data. Over recent years, numerous studies have successfully investigated genetic structure in wild populations using MIS (e.g., Norman et al., 2017; Russello et al., 2015; Steyer et al., 2016). Different approaches have been developed to investigate the genetic structuring of a group or population, using either multivariate analysis (Jombart et al., 2009) or Bayesian methods for optimizing population features such as Hardy-Weinberg equilibrium (Pritchard et al., 2000) and even allowing for the integration of environmental and spatial data for interpretation purpose (e.g., Caye et al., 2015; Guillot et al., 2005). Further, these structure-based approaches are relatively robust in the face of bias related to small sample size or even genotyping error (Smith & Wang, 2014).

Hybridization and introgression

For some species, hybridization and introgression are major threats to population and species persistence creating a need for long-term genetic monitoring (Allendorf et al., 2001). Genetic monitoring approaches using MIS have been applied to detect hybridization in multiple carnivore species including gray wolves (Caniglia et al., 2014; Godinho et al., 2015; Kopaliani et al., 2014; Monzón et al., 2014), Eastern wolves (*Canis lycaon*, Benson et al., 2012), red wolves (*Canis rufus*; Adams et al., 2003; Bohling et al., 2016) and wildcats (*Felix silvestris silvestris*; Anile et al., 2014; Steyer et al., 2016). The majority of these studies have used mitochondrial DNA and microsatellite markers, but a few have used SNPs to detect hybridization or monitor gray wolves (Kraus et al., 2015; Monzón et al., 2014) and

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hybridization between wildcats and domestic cats (Nussberger et al., 2014; Oliveira et al., 2015).

Category II: Population Genetic Parameters

Genetic diversity

Historically, microsatellites were used with MIS to produce estimates of population genetic variation based on allelic diversity and heterozygosity. Allelic diversity, which is often high and variable among microsatellite loci, is not very informative for SNPs. This is because SNPs have comparatively few alleles, generally limited to one or two (i.e., third or fourth alleles at a locus do not materialize before one of the original two is lost due to drift or selection).

On the other hand, estimates of heterozygosity using SNP loci can be more informative than microsatellites because the additional SNP loci surveyed provide higher precision. For example, Doyle et al., (2016) surveyed 162 SNPs in golden eagles and found that mean observed heterozygosity (H_O) was 0.32 ± 0.01 in juveniles whereas adult H_O was 0.35 ± 0.01, a significant statistical difference consistent with expectations of viability selection. Unfortunately, the types of SNP arrays often used in MIS studies preclude the evaluation of other genetic diversity metrics that will likely be important in the future (e.g., runs-of-homozygosity or copy number variants, see Leroy et al, this issue). This is a factor worth considering when planning a study, as evaluating change in genetic diversity metrics over time is an important task of genetic monitoring (see Box 3).

Effective population size

Conservation goals are often set in relation to recent historical abundance, before the impact of anthropogenic activity reduced population sizes. For many species, genetic-diversity based estimates that provide long-term effective population sizes can be the only way to infer

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historical abundance (e.g., Beerli & Felsenstein, 2001). While this approach has its limitations and caveats (Palsbøll et al., 2013), MIS have been used to estimate long-term effective population sizes in species such as southern right whales (Carroll et al., 2015) and Sumatran orangutans (*Pongo abelii*; Nater et al., 2013). Historical samples can provide a direct way of assessing past levels of genetic diversity and effective population size, and therefore any recent changes in these metrics. Although not typically undertaken using MIS, such studies provide important management information for species of conservation concern, for example museum specimens were used to assess historical diversity in species such as grizzly bears (*Ursos actos*; Miller & Waits, 2003) and Seychelles warbler (*Acrocephalus sechellensis*; Spurgin et al., 2014).

Contemporary estimates of effective population size or number of effective breeders are also a critical indication of the genetic resilience of a population (Frankham et al., 2014), and have been estimated with MIS for brown bears (De Barba et al., 2010), Hector's dolphin (*Cephalorhynchus hectori*; Hamner et al., 2017), Eurasian otters (*Lutra lutra*; Koelewijn et al., 2010), and southern right whales (Carroll et al., in review). For the purpose of genetic management of endangered species, the current or contemporary effective size is more relevant than historical or long-term effective size (Wang et al., 2016).

PAST AND FUTURE OPPORTUNITIES

Legacy Datasets

The sheer abundance of microsatellite datasets associated with MIS conservation studies is impressive. Thus, it would be desirable if future monitoring efforts could tie an individual's established microsatellite DNA profile to a new SNP profile. Many individuals of long-lived species like trees, whales, or eagles have already been genetically tagged using microsatellites. In an ideal world, a new DNA profile generated with SNPs would be matched

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to those generated previously with microsatellites. Unfortunately, this is time consuming and expensive because it would require SNP genotyping a reference sample for each individual or having a way to link the SNP genotype to the microsatellite genotype. In principle, it might be possible using a high-density SNP array to genotype individuals at each microsatellite locus. However, in practice, this depends on the availability of the SNPs, the extent of linkage disequilibrium, recombination rates, nucleotide substitution rates, effective population size, as well as the practicalities of designing assays for the repetitive genomic regions that microsatellites represent. In practice, it is an easy decision to forego microsatellites and establish a new SNP array when monitoring a "new" species. There are online tools, such as the ConGress website that contains a Decision Making Tool, that can help managers to identify the optimal path for a MIS analysis (http://www.congressgenetics.eu).

In those cases with extensive legacy datasets, it might make the most sense to use one of the "microsatellite sequencing" techniques in the Table 3 (see above) in an effort to continue surveying the same loci (albeit with a different technology), at the same time as expanding genome sampling. It may be possible to impute genotypes if sufficiently large sample sizes are available for present and past data, and both legacy and modern platforms, as is routinely carried out for individuals types using different SNP panels in livestock species (e.g., Druet et al., 2010). As an example, the imputation of 12 microsatellite markers based on SNP haplotypes has been investigated in cattle, a set of 982 SNPs, located within 500 kb of the targeted markers, being required for accurate imputation (McClure et al., 2012, 2014).

Such imputation is likely to be far more difficult in wild species that lack pedigrees and dense marker panels. That said, it might be possible to use known or suspected relationships among individuals (e.g., full-siblings) to leverage microsatellite-based fingerprinting against SNP-based fingerprinting.

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Future Directions

Evolving technology means that genetic monitoring of populations is expanding beyond SNP genotypes. We broadly categorise these methods into those that will help enhance understanding of population demography, health and diet, and 'functional' or adaptive genetic monitoring (Category III), which moves beyond using neutral alleles for individual identification and estimation of population genetic parameters to assay loci linked to processes such as inbreeding and adaptation (Table 3). Wildlife forensics is also set to benefit from technological advances (see Box 4).

Population demography

Estimating the chronological age of individuals through genetic monitoring would provide broader insights into population dynamics. Age classes, or the chronological age of individuals in a population, are a critical component to estimating past and future growth rates, as well as population level responses to biotic (e.g. prey resources) and abiotic (e.g. hunting) pressures. Conventionally, longitudinal studies that track individuals in well-studied populations have been the only way to estimate age for many species (Clutton-Brock & Sheldon, 2010). However, molecular age biomarkers (MAB), those derived from measurable changes in DNA or RNA abundance or sequence change, offer a new way to estimate chronological age. One MAB that held promise was telomeres, and although it has been found to work well in some bird species (e.g., Haussmann et al., 2003), its wider applicability has been limited (Dunshea et al., 2011). A recent paper showed that epigenetic markers can be used to estimate age in humpback whales (Polanowski et al., 2014), using MIS, an approach that has promise in other species (Jarman et al., 2015).

Epigenetic markers might have utility in monitoring other facets of population demography, as epigenetic changes have been linked to early life conditions (Gapp et al., 2014), reproductive maturity (Lomniczi et al., 2013), survival (Fairlie et al., 2016) and

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response to chemical or physical stressors (Feil & Fraga, 2012), in a variety of species. The development of epigenetic markers therefore has the potential to monitor how environmental processes can influence population demography through monitoring development and fecundity over time.

Health and Diet

The microbial communities living on or in multicellular organisms or 'hosts', termed microbiomes, are a rich area of study in humans and, increasingly, wild animals. Host health and fitness can be affected by the microbiome through different mechanisms: the microbiome could act directly to protect health, through competitive exclusion or by stimulating immunity, or act indirectly, by modifying metabolism or development (Bahrndorff et al., 2016). For example, research has linked changes in skin bacterial microbiome with outbreaks of chytrid fungus in endangered frog populations (e.g., Jani & Briggs, 2014), and there is evidence that symbiotic bacteria on amphibian skin generate metabolites protective against the fungus (Loudon et al., 2014). Additionally, the microbiome might include known pathogens (Acevedo-Whitehouse et al., 2010; Delgado et al., 2017): long-term, non-invasive monitoring of the of the southern resident killer whale population in North America showed that antibiotic resistant bacteria were present in the respiratory microbiome of apparently healthy individuals (Raverty et al., 2017). Therefore, microbiomes could be regularly screened using MIS for the presence of both beneficial and harmful components as part of an ongoing genetic monitoring scheme. Changes in the characteristics of the microbiome over time might also be indicative of changes in the quality of the social or broader environment (Amato et al., 2013; Tung et al., 2015), and can be significantly differentiated amongst individuals within a population (Klein-Jöbstl et al. 2015). Additionally, studies in model organisms have used proteomic analysis of faecal samples to noninvasively monitor host-

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microbe interaction during development (e.g., Young et al., 2015) and disease processes (e.g., Yau et al., 2013).

As the gut microbiome is closely related to diet (Amato et al., 2013; Delsuc et al., 2014), it has been suggested as a potential screening tool to identify dietary components (Bahrndorff et al., 2016). However, evidence suggests that survey methods focusing on non-invasively collected faecal samples need to carefully consider the change in microbiome linked to environmental conditions, time since deposition and focal species (Menke et al., 2015).

While gut microbiome and microbiome-host interaction analysis may be a future method for monitoring diet and health, DNA metabarcoding combined with high throughout sequencing has proven to be an effective genetic monitoring tool to characterize diet (Pompanon et al., 2012; Valentini et al., 2009). This method has been used to non-invasively monitor diet in a diverse range of species including Adelie penguins (*Pygoscelis adeliae*; Jarman et al., 2013), golden-crowned sifaka (*Propithecus tattersalli*; Quéméré et al., 2013) , tapir (*Tapirus terrestris*; Hibert et al., 2013), brown bears (De Barba et al., 2013; Valentini et al., 2009), golden marmots (*Marmota caudata*; Valentini et al., 2009), African herbivores (Kartzinel et al., 2015), Hawaiin tree snails (*Achatinella* spp.; O'Rorke et al., 2015; Price et al., 2017) and leopard cats (*Prionailurus bengalensis*; Shehzad et al., 2012). Limitations of this approach can include a lack of reference samples against which to compare generated data and the fact that findings should be considered semi-quantitative, due to biases such as preferential digestion, PCR amplification bias and gene copy variation (Deagle et al., 2010; Pompanon et al., 2012). However, a metagenomic approach whereby shotgun sequencing is used to characterize both prey and potential pathogens in faecal samples holds the potential to simultaneously characterize diet and microbiomes, while avoiding some of these limitations (Srivathsan et al., 2016). In a broader context, assaying dietary niche through genetic

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monitoring techniques is likely to play a future role in determining the vulnerability of populations to disturbances (Clare, 2014) and is already aiding restoration and relocation plans (Price et al., 2017).

Functional or adaptive genetic monitoring

Traditional genetic monitoring has focused on presumably neutral markers to identify individuals and to assess genetic diversity. When whole-genome data are available, investigators have the choice of using intergenic SNPs from gene deserts or of using "non-neutral" markers derived from protein-coding genes thought to be targets of natural selection (DeWoody et al., 2017; Doyle et al., 2016). This can be an important distinction, because the non-neutral loci are often more sensitive indicators of population differentiation (Freamo et al., 2011). By combining genomic and environmental data, landscape genomics approaches can also be a powerful approach to infer and define conservation units (Funk et al., 2012).

Only a few studies have yet investigated the possibilities of using MIS approaches for such a purpose. Russello et al., (2015) used hair samples to investigate genetic diversity and in the American pika hair, detecting several candidate gene regions which exhibited putative signatures of divergent selection for adaptation to altitude. Given the potential environment shifts related to climate change that can be expected, landscape genomics may offer useful insight to better monitor and manage wild and domestic population.

Conclusion

Genetic monitoring with MIS has proven to be a valuable tool to monitor and manage species and populations. With increasing access to new technological advances, researchers will be able to go beyond identifying individuals to investigate their role in the ecosystem and assess population level dynamics. Such tools will be necessary to meet the challenges of conservation biology in a rapidly changing environment.

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Acknowledgements: This work was assisted through participation in the Next Generation Genetic Monitoring Investigative Workshop at the National Institute for Mathematical and Biological Synthesis, sponsored by the National Science Foundation through NSF Award #DBI-1300426, with additional support from The University of Tennessee, Knoxville. The work arose as part of the intro-population working group that came from this workshop. The authors would like to thank the French Government for providing for the secondment of Dr Gregoire Leroy to FAO. ELC was supported by a Marie Slodowska Curie Fellowship, (Behaviour-Connect) funded by the EU Horizon2020 program. MWB was supported by a Royal Society Wolfson research merit award. LW was supported by the University of Idaho. This research was supported in part by NSF awards 1355106 and 1357386 to AES.
Animal shapes in Boxes 1 and 2 are from www.phylopic.org and under Public Domain and Creative Commons licenses, that can be reused with the following acknowledgements: whale shark; Scarlet23 (vectorized by T. Michael Keesey), elephant; T. Michael Keesey; ostrich: Matt Martyniuk (vectorized by T. Michael Keesey).

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1 Table 1: Contemporary approaches for SNP genotyping of low quality and/or quantity DNA samples.

Reference	Starting material	Species	Platform/method	Inference
SNP Arrays				
Morin and McCarthy (2007)	Bone	Bowhead whale (*Balaena mysticetus*)	Ampliflour SNP genotyping	Development/validation of SNP markers
Mesnick et al., (2011)	Skin	Sperm whale (*Physeter macroephalus*)	Ampliflour SNP and microsatellite genotyping	Population structure
DeWoody et al., 2017	Skin	Gray whale (*Eschrichtius robustus*)	Fluidigm	Individual ID and relatedness
Nussberger et al., (2014)	Hair	European wildcat (*Felis silvestris silvestris*)	Fluidigm	Validation of SNP markers and studying introgression
Ruegg et al., (2014)	Feathers	Wilson's warbler (*Cardellina pusilla*)	Fluidigm	Tracking migratory populations
Kraus et al., (2015)	Faeces	Gray wolf (*Canis lupus*)	Fluidigm	Development/validation of SNP markers
Norman and Sprong (2015)	Faeces	Brown bear (*Ursus arctos*)	Fluidigm	Reconstructing pedigrees and estimating dispersal
Doyle et al., (2016); Katzner et al., (2016)	Feathers	Golden eagle (*Aquila chrysaetos*)	Fluidigm	Population structure, parentage, and provenance
Stetz et al., (2016)	Faeces	River otter (*Lontra canadensis*)	Fluidigm	Development/validation of markers, population assignment
Spitzer et al., (2016)	Faeces	Brown bear (*Ursus arctos*)	Fluidigm	Pedigree and population size estimation
Monzon et al., (2014)	Faeces	Coyote (*Canis latrans*)	Illumina GoldenGate genotyping assay BeadXpress platform	Admixture and hybridisation
Hoffman et al., (2012)	Skin	Antarctic fur seal (*Arctocephalus gazella*)	Illumina GoldenGate genotyping assay	Development/validation of markers
Goossens et al., (2016)	Faeces	Asian elephant (*Elephas maximus*)	MassARRAY (Sequenom)	Population structure and genetic diversity, comparison

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				of SNPs with microsatellites
Fitak et al., (2015)	Faeces	Pumas (*Puma concolor*)	MassARRAY (Sequenom)	Development/validation of SNP markers
Fabbri et al., (2012)	Faeces	Gray wolf (*Canis lupus*)	SNPs Pyrosequencing (Biotage), SNaPshot (ABI), Taqman (ABI)	Development/validation of markers
Targeted sequence capture				
De Barba et al., (2016)	Faeces	Brown bear (*Ursus arctos*)	High-throughput sequencing of microsatellites (Illumina MiSeq)	Development/validation of markers
Perry et al., (2010)	Faeces	Chimpanzees (*Pan troglodytes*)	RNA bait capture/illumina sequencing (Agilent's SureSelect)	Validation/SNP genotyping for genetic diversity
Synder-Mackler et al., (2016)	Faeces	Baboons (*Papio papio*)	RNA bait capture/illumina sequencing	Development/validation of markers, pedigree analysis
Other examples				
Russello et al., (2015)	Hair	American pika (*Ochotona princeps*)	nextRAD	Population structure and outlier loci analysis
Chiou & Bergey (2015)	Faeces	Baboons (*Papio papio*)	ddRAD using FecalSeq	Development/validation of markers

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Table 2. Selective summary of characteristics of next-generation sequencing platforms that could be suitable for low quality or quantity DNA templates frequently obtained during MIS projects.

Platform	Development Cost	Run cost	Effort (after DNA extraction)	Information	Error rate	DNA required	Ref
Fluidigm	€4300 for oligos to query 96 SNPs, access to Fluidigm system	€1250 for genotyping 96 individuals at 96 SNPs	PCR	SNP genotype	~1% [A]	Nanograms	Doyle et al., (2016), Katzner et al., (2016), DeWoody et al., (2017)
Amplifluor	€2200 for oligos for 96 loci, access to qPCR machine	€250 for genotyping 96 samples at 96 loci, based on 20 loci multiplex*	PCR and analysis of qPCR results	SNP genotype	1.4% [B]	Nanograms	Mesnick et al., (2011)
MassARRAY	€2600 for oligos for 96 loci, assuming 2 alleles per locus, access to MassARRAY system	€777 (384 well format, €8.09 per sample) to €1,376 (96 well format, €14.33 per sample) to genotype 96 individuals at 96 SNPs (24-loci multiplex)	Multiplex PCR step, clean up step, primer extension step and another clean up step, run on compact mass spectrometer	SNP genotypes	Fecal sample error rate: 24-loci multiplex 9%; 42-loci multiplex error rate: 25% [A]	nanograms (10 ng per multiplex reaction recommended)	Goosens et al., (2016)
GTSeq	<€9000: primary cost is oligos but a pilot study of the markers is	€3.43 per sample, based on example where 2068 samples	For each of the 22 x 96-well plates there were 2 PCR steps and one	SNPs; could be extended to haplotypes	0.01% [C]	Nanograms (10 ng for first PCR minimum recommended	Campbell et al., (2015) , N. Campbell,

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	suggested, high-throughput sequencing run	were genotyped at 192 loci	normalisation step			concentration)	pers. comm.
Microsatellite sequencing	Primary costs are optimization and validation study, as well as oligonucleotides	No estimate provided	Multiplex PCR, purification and quantification of pooled PCR product and sequencing run	Microsatellite genotypes	Good quality reference hair: allelic dropout (ADO): 3.9%, false allele rate (FA): 0.3%, Non-invasively collected low quality hair: ADO: 10.6%, FA 0.8%; Low quality faecal samples: ADO: 13.7%, FA: 0.8%[C]	Not quantified in study	De Barba et al., (2016)

*Based on purchase of 5000 assay kit

Error rate reported are based on replicate genotyping[A] or calculated per allele[B] or per locus[C]

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Table 3: Beyond genotypes: selected examples of the application of genomic sequencing technology to study ecology and evolution of species using minimally invasive samples.

Reference	Starting material	Species	Platform/method	Inference
Assessing genetic diversity				
Hans et al., (2015)	Faeces	Gorilla (*Gorilla gorilla*)	Illumina MiSeq of pooled PCR amplicons	Diversity of MHC loci
Ang et al., (2016)	Faeces	Tonkin snub-nosed monkey (*Rhinopithecus avunculus*)	Illumina HiSeq of pooled PCR amplicons	Diversity of mtDNA
Sigsgaard et al., (2016)	eDNA water sample	Whale shark (*Rhincodon typus*)	Illumina MiSeq (bulk sequencing)	MtDNA haplotype diversity and identity
Health/diet/demography				
Valentini et al., (2009)	Faeces	Golden marmots (*Marmota caudata*) and brown bears (*Ursus arctos*)	454 sequencing of PCR amplicons	Diet
Shehzad et al., (2012)	Faeces	Leopard cat (*Prionailurus bengalensis*)	Illumina PCR amplicon sequencing	Diet
Jarman et al., (2013)	Faeces	Adelie penguin (*Pygoscelis adeliae*)	Ion Torrent PCR amplicon sequencing	Diet
De Barba et al., (2014)	Faeces	Brown bear (*Ursus arctos*)	Illumina PCR amplicon sequencing	Diet
Quéméré et al., (2013)	Faeces	Golden-crowned sifaka (*Propithecus tattersalli*)	Illumina PCR amplicon sequencing	Diet
Polanowski et al., (2014)	Skin biopsy sample	Humpback whale (*Megaptera novaeangliae*)	Bisulfite conversion and PYROMARK 24 Pyrosequencing platform (Qiagen)	Estimate of chronological age
Kartzinel et al., (2015)	Faeces	Seven large mammalian herbivores	Illumina PCR amplicon sequencing	Diet and niche partitioning
O'Rorke et al., (2015); Price et al., (2017)	Faeces	Hawaiian tree snails (*Achatinella* spp.)	Illumina PCR amplicon sequencing	Diet and niche partitioning,

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				environmental restoration planning
Srivathsan et al., (2016)	Faeces	Banded leaf monkey (*Presbytis femoralis*)	mtDNA shotgun sequencing Illumina HiSeq	Diet and gut parasite characterisation
Raverty et al., (2017)	Exhaled breath samples	Killer whale (*Orcinus orca*)	PCR amplicon sequencing of bacterial DNA barcodes and direct culture of bacteria	Genetic monitoring of respiratory microbiome

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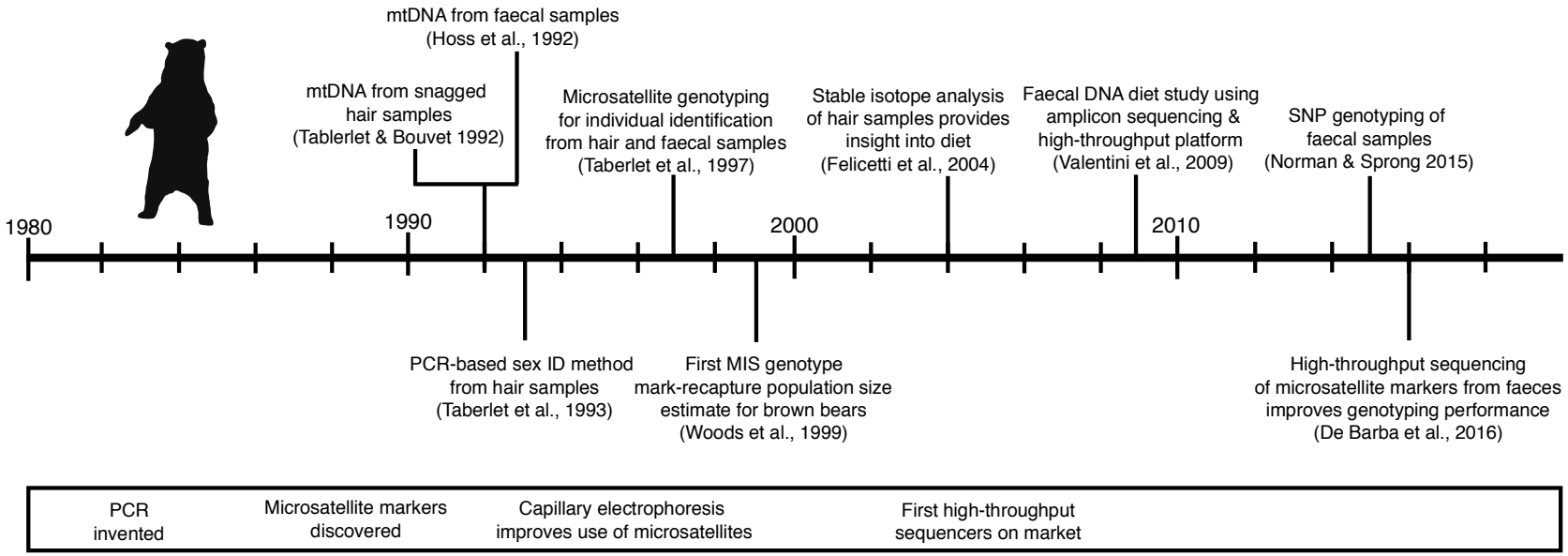
1 **BOXES**

2 **Box 1: Brown bears (*Ursus arctos*) as a Model System for the Development of MIS Approaches**



3

4 The brown bear is the most widely distributed bear species and is locally endangered at many locations across its range. The desire for alternative

5 methods to monitor this charismatic species launched the field of noninvasive genetic sampling, and the field has kept pace with technological

6 developments. First, Taberlet & Bouvet (1992) and Hoss et al., (1992) demonstrated that mitochondrial DNA (mtDNA) sequences could be

7 obtained from snagged hair and faecal samples, respectively. Hoss et al., (1992) were also the first to demonstrate the ability to amplify diet

8 items in scat by sequencing a 356 bp *rbcL* chloroplast sequence to identify the dominant plant in their diet (*Photinia villosa*). These were the first

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studies to document successful amplification of DNA from hair and fecal samples of wild species. Soon researchers were amplifying nuclear DNA to determine sex (Taberlet et al., 1993) and for individual identification (Taberlet et al., 1997). This work was critical to the understanding of microsatellite genotyping errors and approaches for minimizing their impact in MIS datasets (Taberlet et al., 1996). MIS was then used extensively in Europe in the 1990s to obtain data on genetic diversity, genetic structure, phylogeography and minimum counts of population size (Kohn et al., 1995; Taberlet et al., 1997, 1992) . In the late 1990s, North American researchers embraced MIS methods as an alternative approach for population estimation and produced the first mark-recapture population estimates using DNA extracted from brown bear hair samples collected from barbed-wire hair snares (Mowat & Strobeck, 2000; Woods, 1999), which revolutionized methods for estimating population size (Boulanger et al., 2004; Kendall, 2009). This approach was expanded to include stable isotope analysis of hair samples to provide a new approach for noninvasively determine the number of brown bears in Yellowstone park feeding on cutthroat trout and estimate the number of fish consumed per year by bears (Felicetti et al., 2004; Haroldson et al., 2005; Teisberg et al., 2014). MIS applications have expanded to include obtaining DNA from saliva on mammalian (Farley et al., 2014) and salmonid (Wheat et al., 2016) carcasses to conduct species and individual identification. MIS has been the main method used to track small remnant or reintroduced populations in Europe (e.g., De Barba, 2010; Karamanlidis et al., 2010), Pakistan (Bellemain et al., 2007), western continental United States (Proctor et al., 2012; Romain-Bondi et al., 2004) and the Gobi desert (McCarthy et al., 2009; Tumendemberel et al., 2015). Brown bears have also been an important model system for the transition from genetic to genomic approaches in MIS. For example, they have been the focus of dietary metabarcoding studies (De Barba et al., 2013; Valentini et al., 2009). Recently, new approaches were developed to sequence PCR-amplified microsatellites on an Illumina platform to

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obtain multilocus genotypes from brown bears (De Barba et al., 2016). This approach increased success rates by 20-30% and decreased costs per sample by 40% compared to traditional capillary electrophoresis genotyping of microsatellite loci. Also, SNP loci have been identified for brown bears and successfully genotyped for faecal samples using the Fluidigm platform (Norman & Sprong, 2015; Spitzer et al., 2016). These advancements using genomic methods provide much promise for the continued noninvasive genetic monitoring of brown bears across their range. The figure shows the timeline of the key advances in using MIS for genetic monitoring of brown bears, along with the approximate timing of some key molecular methods.

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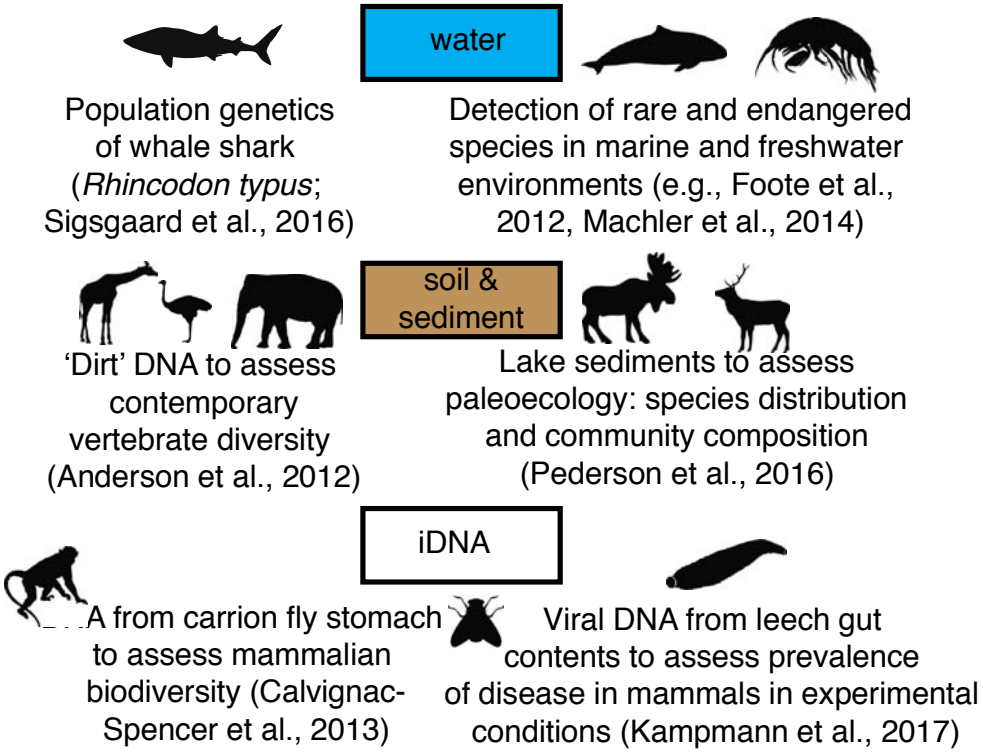
Box 2: Environmental DNA in the genetic monitoring context

Genomic sequencing technologies are broadening the scope of eDNA studies in genetic monitoring. Historically, eDNA samples have included hair, faeces and feathers. Now the scope is expanding to include environmental samples including water, soil, sediments, snow, browsed foliage, as well as DNA from invertebrates ("iDNA"; Schnell et al., 2015) that feed on species of interest: some examples are illustrated below.



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Box 3: The importance of 'delta' in genetic monitoring

Endangered species are, by definition, the subject of local, regional, national and international legislation, including the Convention on Biological Diversity (CBD). The CBD's 2020 Targets include a commitment to '*minimise genetic erosion*' and '*safeguard genetic diversity*' (Bruford et al., 2017; Hoban et al., 2013). These commitments require a means of verification and imply a reference point from which to determine changes in genetic diversity. The statistical approaches needed to evaluate changes in genetic diversity over short timescales, however, require development. Temporal genetic monitoring of species at the same location has been accomplished in a some well-studied populations or species of high conservation concern (e.g., Italian brown bears; De Barba, 2010) (e.g., Māui's dolphin; Baker et al., 2016) or where hybridisation is a threat (e.g., red wolves and coyotes; Bohling, 2016).

In the absence of samples from a population over time, analysis of genetic data using single point samples can provide insights into recent demographic change (e.g., Goossens et al., 2006), however single point estimators can have wide variance and provide inconsistent values depending on the methods chosen or model assumptions (Barker, 2011). Hoban et al., (2014) carried out an assessment of temporal indicators of genetic erosion (*sensu* Aichi Target 13) to assess which metrics and sampling would be the most sensitive to detecting short-term declines in genetic diversity. The number of alleles per genetic locus outperformed all other potential indicators across all scenarios.

Sampling 50 individuals at as few as two time points with 20 microsatellite markers could detect genetic erosion even in cases where 80– 90 % of diversity remained (Hoban et al 2014).

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Power increased substantially with more samples or markers, with, for example, 2500 SNPs being extremely effective at detecting minor demographic declines. Hoban et al., (2014) also found that statistical power to detect change improved if samples were available before the onset of decline, implying that archived and museum collections can clearly play an important role as part of monitoring programs.

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Box 4: Wildlife Forensics

As the global threat of illegal wildlife trade becomes more apparent, the use of genetic and genomic tools in the fight against wildlife crime has increased substantially (Corlett et al., 2017; Ogden & Linacre, 2015; Staats et al., 2016). Traditional genetic tools are increasingly being applied to forensic casework involving material inherently lacking in viable genetic material, e.g. microsatellite markers to locate the likely origin of seized elephant ivory (e.g., Wasser et al., 2015), and similar tools are now in routine use to enable the development of a database to allow the matching of carcasses and seized, poached African rhinoceros horn (Harper et al., 2013). DNA barcoding is being increasingly used in the identification of traded products to species, such as pangolin scales (Mwale et al., 2017).

The use of genomics has, however, opened up the possibility of additional applications in the forensic field, including the development of simple, cost effective tools to analyse extremely problematic samples and to address questions that were otherwise statistically unattainable using standard genetic approaches. For example, it is possible to identify putrid bushmeat samples, which can be highly degraded once seized, to species level or beyond using low cost microarrays, (e.g. Ronn et al, 2009). A landmark paper in 2011 developed a set of SNPs for investigation of false eco-certification of exploited European fish stocks using population assignment that relies on divergent SNPs under the influence of selection in species in otherwise undifferentiated populations, where standard microsatellite-based population assignment had proved impossible (Nielsen et al., 2012). Furthermore, portable sequencing devices, such as the MinIon (Oxford Nanopore Technologies), are starting to be used to sequence samples in field laboratory conditions (Edwards et al., 2016; Quick et al., 2016). This leads to the possibility real-time assessments of the species and potentially population of origin of products in markets in the near future.

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