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SPECIAL REVIEWS IN ORNITHOLOGY

GENETIC APPLICATIONS IN AVIAN CONSERVATION

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A FUNDAMENTAL NEED in conserving species and their habitats is defining distinct entities that range from individuals to species to ecosystems and beyond (Table 1; Ryder 1986, Moritz 1994, Mayden and Wood 1995, Haig and Avise 1996, Hazevoet 1996, Palumbi and Cipriano 1998, Hebert et al. 2004, Mace 2004, Wheeler et al. 2004, Armstrong and Ball 2005, Baker 2008, Ellis et al. 2010, Winker and Haig 2010). Rapid progression in this interdisciplinary field continues at an exponential rate; thus, periodic updates on theory, techniques, and applications are important for informing practitioners and consumers of genetic information. Here, we outline conservation topics for which genetic information can be helpful, provide examples of where genetic techniques have been used best in avian conservation, and point to current technical bottlenecks that prevent better use of genomics to resolve conservation issues related to birds. We hope this review will provide geneticists and avian ecologists with a mutually beneficial dialogue on how this integrated field can solve current and future problems.

TAXONOMY

If conservation strives to preserve as much variation as possible at all levels of biodiversity, then conservation depends upon taxonomy. Whether conservation priorities are based on species, subspecies, or evolutionarily significant units (ESUs), DNA is increasingly being used to determine the evolutionary and geographic boundaries of these entities. Far from merely academic considerations, these groupings are critically important in conservation prioritization and can have important legal ramifications for threatened and endangered species, subspecies, distinct population segments (DPSs), or ESUs (reviewed in Haig et al. 2006, Garnett and Christidis 2007, Haig and D'Elia 2010). Despite the importance of defining these units, boundaries of species, subspecies, and populations are not always clear, and hybridization can further conflate taxonomic analyses and conservation options (Haig and Allendorf 2006). Advances in conservation genetics have proved helpful in resolving some long-standing taxonomic questions in birds, but philosophical disagreements over fundamental taxonomic concepts remain.

Species.—Although birds are arguably the best-studied vertebrate group, vigorous debate continues over which species definition best applies to them. The three top contenders include the biological species concept (BSC; see Tobias et al. 2010, Winker 2010a)—the most commonly used in avian taxonomy—and two that have emerged from cladistics (the phylogenetic and monophyletic species concepts; Cracraft 1983, 1992; Mishler and Brandon 1987; McKitrick and Zink 1988; Zink and McKitrick 1995). In part because of the multiplicity of applied species concepts, avian taxonomy is far from stable at any level, and this has real-world conservation implications. For example, patterns of endemism in the birds of Mexico (Peterson and Navarro-Sigüenza 1999) and the Philippines (Peterson 2006) depend on whether a biological or phylogenetic species concept is used. The use of different species concepts has also been shown to affect the composition of lists of endangered birds in Mexico (Rojas-Soto et al. 2010), and vigorous discussion regarding the appropriateness of splitting polytypic species continues (Christidis and Boles 2008, Chesser et al. 2010). At the same time, new dialogues are emerging about the importance of studying speciation patterns in migratory birds, given that differentiation and speciation appear to be common even in the absence of extended isolation (Winker 2010b).

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TABLE 1. Issues addressed by avian conservation genetics.

Taxonomy	(Meta) populations	Landscapes
• What are the evolutionary and geographic boundaries of species, subspecies, and management units? • What is the extent of introgression or hybridization? • Which species are represented in illegal wildlife trade? • What cryptic species have been misclassified? • How is biodiversity changing in response to climate change? • What is the identity of a hybrid, cryptic specimen, or the remains of an ancient or recent specimen? • What is the best avian tree of life for prioritizing biodiversity conservation by phylogenetic diversity?	• What are levels of genetic diversity, population structure, effective population size, or gene flow and how have they changed over time? • What is the best strategy for managing small populations to maximize conservation of genetic diversity (pedigree analyses)? • What is the extent of population connectivity or isolation? • Which populations would be the best source for a translocation or reintroduction? • How do individuals and populations move throughout the annual cycle? • How are disease transmission pathways linked to bird movements?	• What are the effects of landscape features and landscape heterogeneity on genetic diversity and population structure? • How are phylogeographic patterns of birds changing in response to climate change? • Which populations or life stages are most affected by contaminant exposure; are certain genotypes more vulnerable? • In mixed-stock populations, what proportion of each stock is being harvested or affected by environmental perturbations?

While debate over species concepts endures, the increasing ease and affordability of DNA sequence analysis provides new power for discriminating among morphologically similar taxa, and continues to change our understanding of avian taxonomy (insets 1 and 2; Bickford et al. 2007). Nearly all easily recognized bird species were thought to be described decades or centuries ago, leading ornithologists to conclude by the 1950s that there were few undiscovered bird species or geographic races (Zimmer and Mayr 1943, Stresemann 1975). However, continued discovery of new avian taxa into the 21st century indicates that conclusion to have been premature. Just within the antbirds (Thamnophilidae), the American Ornithologists' Union (AOU) has recognized an additional 15 species since 1983 and elevated 12 subspecies to full species status while lumping just two species together (Remsen et al. 2010).

Genetic analyses have been critical to most recent discoveries of new birds because these are usually cryptic species with subtle or indistinguishable external characters resulting from evolutionarily conservative morphology, a reliance on nonvisual mating cues, or convergent morphological evolution (Bickford et al. 2007, Trontelj and Fišer 2008). In the case of the Gray-crowned Palm-Tanager (*Phaenicophilus poliocephalus*), Sly et al.'s (2010) identification of two taxa, with one being Haiti's only endemic bird, led to renewed interest in protecting a threatened biodiversity hotspot on the Tiburon Peninsula. Studies of tapaculos in the genus *Scytalopus* (Rhinocryptidae) also demonstrate the ability of genetic data to reveal unrecognized biodiversity. These small mouse-like birds of the Andes and southeastern Brazil inhabit the dark undergrowth of forests and scrub. *Scytalopus* song has often been used to define species' limits because their morphology is so static over evolutionary time that they often vary more within than among species (Krabbe and Schulenberg 2003). Thus, it was quite surprising when Maurício et al. (2008) tested *Scyatlopus* monophyly with molecular data and discovered a cryptic genus, *Eleoscytalopus*. Subsequently, Mata et al. (2009) used mitochondrial and nuclear DNA sequences to reveal four potential cryptic species, one within the White-breasted Tapaculo (*E. indigoticus*) and three within the Mouse-colored Tapaculo (*S. speluncae*).

Once putative cryptic species are identified with genetics, analyses of song and closer inspection of morphology often provide additional support for the species status. However, species will not always diverge equally in all character systems, as demonstrated by recent studies of warbler finches (*Certhidea*) in the Galápagos. These morphologically conservative birds are the most basal and widespread of Darwin's finches and do not exhibit any premating isolation due to song, so they have traditionally been treated as one species (Grant and Grant 2002). Recent discovery of large intraspecific genetic differences resulted in recognition of two species (*C. olivacea* and *C. fusca*; Freeland and Boag 1999, Petren et al. 1999). These genetic differences were not correlated with geography, as in most cases of cryptic diversity, but were instead associated with habitat differences (Tonnis et al. 2005).

Many have pointed out that using multiple lines of evidence (DNA, song, morphology, ecology, etc.) in taxonomic decisions may lead to incongruent results (Zink 1989, O'Brien and Mayr 1991, Ball and Avise 1992, Zink 2004), leading some to advocate use of mitochondrial DNA (mtDNA) over other data in making such delineations (Ball and Avise 1992, Zink et al. 2000, Zink 2004). Others have emphasized the need for multilocus data (Edwards and Beerli 2000) and more inclusive approaches that combine genetic data with data from plumage, morphology, song, and behavior (Dizon et al. 1992, Vogler and DeSalle 1994, Haig et al. 2006, Alström et al. 2008). Tobias et al. (2010) took this a step further and proposed using a scoring system based on biometrics, plumage, and song to measure divergence between undisputed sympatric species as a yardstick for assessing the taxonomic status of allopatric forms. Although it needs further testing, their approach yielded relatively few changes to avian taxonomy in Europe. They argued that the benefits of this approach include a systematic and defensible approach that can

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HIGH-THROUGHPUT SEQUENCING AND SINGLE-NUCLEOTIDE POLYMORPHISMS

High-throughput sequencing technology offers the capacity to quickly collect a tremendous amount of genetic data from select individuals (Hudson 2008) and has created a new gold standard for multilocus data sets that sample across many unlinked portions of the genome (Mardis 2008, Lerner and Fleischer 2010). The analytical power afforded by large genetic data sets is revolutionizing genomic studies of birds at every spatial and temporal scale (Edwards et al. 2005, Hackett et al. 2008, Jennings et al. 2011). Where previous avian population or phylogeographic studies might employ 8 to 10 variable microsatellite loci at best, now hundreds of thousands of variable loci are easily attainable and at far lower costs in supplies and personnel.

Molecular markers used in traditional studies were thought to be selectively neutral and sampled only a minute portion of the genome, particularly in avian studies. A limitation of such studies, however, lies in their assumptions that the detected level of neutral genetic variation in a population is correlated with levels of functionally important variation and that low levels of functional variation lead to low fitness and low ability to adapt to future change. High-throughput sequencing and other advances in genomics allow for not only the expansion of the amount of the genome examined but also the detection and characterization of functional genes that are responsible for survival and adaptation.

This new ability to scan the entire genome for variation is extremely useful in genomic studies, as in cases where nominal subspecies of birds differ greatly in morphology, song, or behavior but not in the sequence of commonly used molecular markers such as cytochrome *b* or cytochrome oxidase I (Zink 2004). In some cases, genome-wide scans may help pick out fast-evolving loci that contribute to the observed phenotypic differences (for a celebrated example in mice, see Hoekstra et al. 2006), thereby reconciling apparent conflict between molecules and morphology.

Conversely, the success of many recent studies in employing a concise set of mitochondrial and nuclear markers to delineate species and subspecies (Barrowclough et al. 2004, Oyler-McCance et al. 2005b, Peters et al. 2005, Barker et al. 2008, Ross et al. 2010) and the multiplicity of available methods for species delimitation (Sites and Marshall 2003, Wiens 2007) demonstrate that solid taxonomic conclusions can be drawn from small fractions of the genome. In that light, traditional Sanger sequencing of many individuals for relatively few, carefully chosen loci may continue to present a cost-effective approach to problems in taxonomy for many years to come. However, next-generation high-throughput sequencing represents an important new addition to the conservation genetic toolbox.

Perhaps the newest aspect of utilizing high-throughput sequencing for avian conservation geneticists is the use of single-nucleotide polymorphisms (SNPs; Fig. 1). SNPs are the most abundant type of genetic polymorphism in any genome, and those found within a coding sequence are of particular interest because they are more likely to alter the biological function of a protein. Although an individual SNP has limited polymorphism (there are only four states given the two nuceleotides), use of high-throughput sequencing provides easy access to the development of hundreds of SNPs for a particular study. Thus, they are increasingly being used as markers in natural population studies because they provide an opportunity to assess a large number of unlinked loci for a range of questions (Slate et al. 2009). However, SNP use in avian studies is just beginning: their distribution, linkage mapping, and so on have been investigated only recently (Backström et al. 2006, 2008; Kimball et al. 2009). Precious few avian conservation studies have used SNPs thus far. García and Arruga (2006) used SNPs to differentiate species of partridges for reintroduction, and Väli et al. (2010) used them to examine hybridization between two species of spotted eagles in Europe. Clearly, the future is upon us, given the power of high-throughput sequencing and the associated power utility of SNPs.

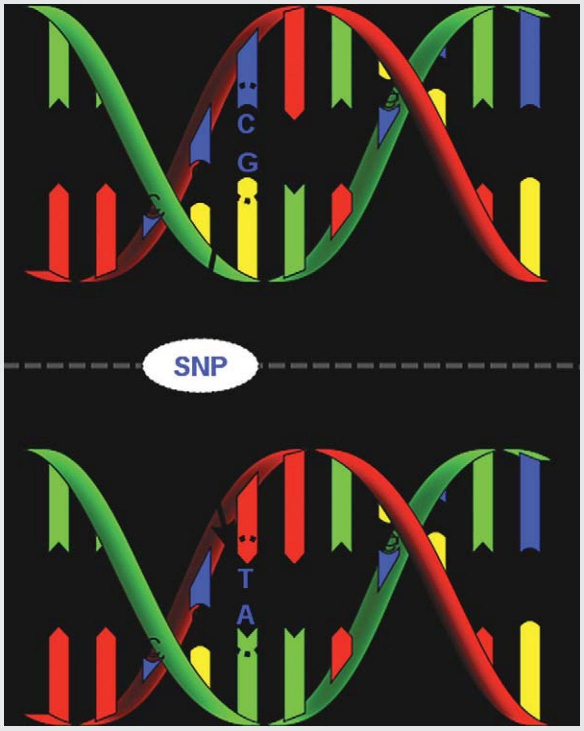

Fig. 1. A single-nucleotide polymorphism (SNP) is a DNA sequence variation that occurs when a single nucleotide differs between members of a species or paired chromosomes in an individual. Thus, it is a change of a nucleotide at a single base-pair location on DNA. In the example shown here, two sequenced DNA fragments from different individuals contain a difference in a single nucleotide (*AAGC**C**TA* to *AAGC**T**TA*). Therefore, there are two alleles: ***C*** and ***T***. Most SNPs have only two alleles. (Figure by D. Hall.)

be applied across taxa worldwide. This sort of methodology, expanded to include genetic data, could benefit conservation by providing a consistent approach that includes multiple lines of taxonomic evidence by combining neutral genetic markers with phenotypic data that likely reflect the influence of reproductive isolation (Haig et al. 2006, Garnett and Christidis 2007). Thus, one may capture variation due to multiple influences on speciation and move toward a taxonomy that best reflects likely separations among gene pools, even when it is not possible to demonstrate strict reproductive isolation.

Two recent investigations exemplify the use of multiple lines of evidence to assess taxonomic boundaries: studies of the

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BARCODING

DNA barcoding is a powerful genetic tool that seeks to sequence specific short portions of the genome (in animals, typically cytochrome oxidase I [COI]) of all organisms on the planet to aid in species identification (Fig. 2; Hebert et al. 2003, Moritz and Cicero 2004, Hebert and Gregory 2005, Ratnasingham and Hebert 2007, Baker et al. 2009). Barcodes promise an easy way to reliably determine species membership even in cases where morphology-based identification is difficult, as in the case of juveniles, isolated feathers, or the remains of birds unlucky enough to be sucked into jet engines. As sequencing becomes less expensive and easier to perform, barcodes also offer a powerful way for non-experts, citizen scientists, and people in the developing world to conduct biodiversity surveys.

Barcoding has attracted major funding over the past decade (see, e.g., www.dnabarcoding.ca/), and the corresponding rise of initiatives such as the Barcode of Life project (www.barcodeoflife.org) sparked debate in taxonomic circles over the relative merit of molecular and morphological approaches to taxonomy (Tautz et al. 2003, Hebert et al. 2004, Wheeler et al. 2004, Will and Rubinoff 2004, DeSalle et al. 2005, Hebert and Gregory 2005, Hajibabaei et al. 2007). In the face of major criticism that the information contained in a single gene could not be used to reliably reconstruct phylogeny or delimit species (Will et al. 2005, Brower 2006, Rubinoff 2006) because of introgression, insufficient signal, incomplete lineage sorting, and various other problems, advocates of barcoding pointed out that barcodes could still yield remarkably reliable identifications for known species, as in a pioneering study of birds that found that COI sequence variation among species typically exceeded variation within species by 18-fold (Hebert et al. 2004). A later, more comprehensive study (Kerr et al. 2007) revealed instances in which COI failed to provide sufficient information to identify all bird species tested, but even so, the success rate was 94%, with difficulties being mostly confined to clusters of recently diverged species or cases of possible hybridization. A similar study found that single-locus barcodes can identify 98% and 93% of known marine and freshwater fishes, respectively (Ward et al 2009). Even most pairs of sister species can be reliably separated by COI barcodes (Hebert et al. 2004, Tavares and Baker 2008). On the basis of those successes, broad utility of the approach for assigning unknown individuals to known species is now accepted by many, but there are still important caveats. The barcoding approach relies on the existence of a comprehensive reference database (Ekrem et al. 2007), and such databases can be misled by the presence of nuclear mitochondrial pseudogenes (Song et al. 2008). Furthermore, multiple barcode loci may be required for reliable identification in certain taxa (CBOL Plant Working Group 2009, Kress et al 2009), the barcode method still fails to discriminate a small but important percentage (≤8%) of known species in even well-studied groups (Meyer and Paulay 2005, Kerr et al. 2007, Ward et al. 2009), and the reliability of barcode-based identification declines precipitously in groups that lack a well-studied taxonomy (Meyer and Paulay 2005).

FIG. 2. Color-coded barcodes for the Black Tern (*Chlidonias niger*, top) and the White-winged Tern (*C. leucopterus*, bottom) illustrate the ease with which species can be quickly identified and differentiated. (Image prepared by Kevin Kerr, U.S. National Museum.)

For all its strengths, barcoding is best seen as an enhancement to, and not as a replacement for, conventional taxonomic investigations. Although barcode approaches can recognize whether a test sequence does or does not closely match those already in the database (and thus suggest the presence of a potential new species in the latter case), reliance on barcode data alone can overlook species (Hickerson et al. 2006, Brower 2010), and species delimitation is best accomplished with multiple genes and multiple lines of evidence (Moritz and Cicero 2004, Will et al. 2005). For example, in a recent comprehensive defense of single-locus barcoding, Baker et al. (2009) explicitly stated that "more rigorous methods of species delimitation should be favored using coalescent-based techniques that include tests of chance reciprocal monophyly, and times of lineage separation and sequence divergence." Their statement is far from an indictment of barcode-based approaches to identification; it simply acknowledges that the database underlying barcode identifications should be based on the most rigorous taxonomy and species delimitation possible, and that barcoding can enhance but should never replace the many contributions of trained systematists.

Spotted Bush-Warbler (*Bradypterus thoracicus*) complex by Alström et al. (2008) and studies of the Stripe-headed Brush-Finch (*Arremon torquatus*) complex by Cadena and Cuervo (2010). The former compared plumage, morphology, egg coloration, song, mtDNA haplotypes, habitat–altitudinal distribution, and behavior and suggested that *B. thoracicus*, *B. davidi*, and *B. kashmirensis* should be recognized as full species because they differ in most aspects. Similarly, Cadena and Cuervo (2010) used data from song, morphology, ecology, and genetics to suggest recognition of eight full species in a group formerly treated as a conglomerate of 14 subspecies.

Recent splitting of Greater Sage-Grouse (*C. urophasianus*) into two species (now including Gunnison Sage-Grouse [*C. minimus*]; Young et al. 2000) illustrates how recognition of cryptic species can carry major conservation implications (Hazevoet 1996). The Gunnison Sage-Grouse comprises less than 5,000 individuals, and threats are considered imminent and of high magnitude, whereas the population of Greater Sage-Grouse, although significantly reduced from historical numbers, is still estimated to exceed 100,000 individuals, and threats to this species are considered moderate in magnitude (U.S. Fish and Wildlife Service [USFWS] 2010a, b). Although both species are now considered

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candidates under the U.S. Endangered Species Act (ESA; i.e., they were found to warrant ESA protection but listing is currently precluded by higher-priority listing actions), the Gunnison Sage-Grouse has a higher listing priority than the Greater Sage-Grouse, which means that it is likely to receive ESA protection sooner than the Greater Sage-Grouse, and sooner than it would have if it were listed as a subspecies or DPS. It is also possible, given the higher level of threats and smaller population size, that the Gunnison Sage-Grouse could ultimately receive a higher level of protection under the ESA than the Greater Sage-Grouse.

Subspecies.—While the goal of species conservation is shared by all who value biodiversity, the existence, identification, and conservation of subspecies has received mixed support (Zink 2004, Haig et al. 2006, Haig and D'Elia 2010, Winker and Haig 2010). A "subspecies" is generally defined as a breeding population that has measurably distinguishable genotypes or phenotypes (or both) and occupies a distinct geographic area within its species range (Mayr 1969, Avise 2004, Patten 2010, Remsen 2010). Variation below the species level can embody evolutionary and developmental responses to heterogeneous geography, differential selection, or neutral processes such as bottlenecks and stochasticity. Some of the strongest arguments about the validity of the subspecies concept describe attempts to delineate its upper and lower bounds (Winker 2010a). That is, at what point is geographic variation suitably differentiated to justify subspecific status and at what level of differentiation do recognized subspecies achieve full species status?

Although ornithologists have traditionally defined avian subspecies (and species) using plumage, morphology, and behavior, advances in molecular biology have led to the use of variation in discrete and presumably selectively neutral genetic markers (Winker and Haig 2010). These molecular data provide an additional avenue for taxon delineation, but in many cases the molecular data sets are not congruent with subspecies defined by traditional methods (Zink 1989, 2004; O'Brien and Mayr 1991; Ball and Avise 1992; Burbrink et al. 2000; Funk et al. 2007b; Draheim et al. 2010; Zink et al. 2010). Zink (2004) argued that subspecies defined by traditional nonmolecular methods may actually misinform conservation efforts through misrepresentation of underlying patterns of intraspecific variation. This lack of concordance among approaches has led some to suggest that molecular methods (i.e., reciprocal monophyly among mitochondrial sequences) should be used preferentially to define conservation units (Moritz 1994, Zink 2004). Others suggest that discordance should be expected when using neutral molecular data to examine shallow levels of divergence, as compared with phenotypic data sets that describe variation that is likely reflective of processes that are not selectively neutral (Greenberg et al. 1998, Oyler-McCance et al. 2010, Pruett and Winker 2010, Winker 2010a).

At present, so few described avian subspecies have received examination via modern molecular methods that it is difficult to draw general conclusions about the validity or utility of the subspecies concept (but see Klicka et al. 2011). Thus, new, genetically informed attention to intraspecific variation across a greater taxonomic range is warranted (Haig and Winker 2010, Remsen 2010). As the application of genomic methods become more widespread among avian taxa, examination of the genetic basis for adaptation and phenotypic variation may help sort out the issue (Hoekstra et al. 2006, Mumme et al. 2006, Mitchell-Olds et al. 2007).

Decisions to recognize or not recognize subspecies have significant conservation implications under many endangered-species classification and funding schemes (reviewed in Haig et al. 2006, Haig and D'Elia 2010). For example, there would be no taxonomic units below the species level if the phylogenetic species concept (PSC) were adopted by the AOU. Thus, USFWS, IUCN, COSEWIC (Committee on the Status of Endangered Wildlife in Canada), and others would have to reconsider current avian subspecies listings. In the United States, subspecies would have to be re-examined for listing as either species or some other entity such as a DPS or ESU. Elevation of subspecies to species (under the PSC) could aid conservation efforts because such entities could be given added weight corresponding to their elevated taxonomic status under the IUCN criteria. However, many other difficulties could result. For one, the change could make it more difficult to add species to various endangered-species lists because of the added workload, cost, and, perhaps, public fatigue from hearing about many new species being listed simply because a new species concept has been applied. Furthermore, it could reopen litigation regarding the listings. Swamping the IUCN list with many new "species" could reduce the importance of a former "species" with a wider geographic range. Finally, adopting the PSC and recognizing many more avian species could exacerbate the difficulty of visual identification or differentiation of species by law-enforcement agents around the world who often struggle to identify particular species under even the BSC criteria. Overall, the changes to policy that would arise from adopting the PSC argue neither for nor against the biological validity of that concept, but effectively illustrate that the species-concept debate carries major implications for conservation.

Hybridization.—Hybridization and introgression can result in extinction of native fauna when nonindigenous species are introduced or disperse into novel environments (Rhymer and Simberloff 1996, McCarthy 2006, Mallet 2008). Molecular methods are the fastest and most accurate means of revealing boundaries between known taxonomic entities that are permeable or under erosion, as in the case of hybridization. Allendorf et al. (2001) developed hybrid categorization guidelines to assist with management decisions. These are particularly useful for those species that receive protection under the ESA and where law-enforcement agents need to accurately identify taxa to decide whether or not a violation of the ESA's prohibited acts (ESA section 9) has occurred. Hybrids are not protected under the ESA, IUCN, or SARA (Species at Risk Act), which has caused numerous debates, especially for species listed under the ESA (for review, see Haig and Allendorf 2006). Problems arise when a listed species hybridizes with a nonlisted species and the hybrids are not visually distinguishable from the listed taxa, leaving law-enforcement agents unable to prosecute a person who has harmed or killed the listed species, unless they have access to molecular tools that can sort hybrids from listed species.

Owls in genus *Strix* exemplify the utility of genetic tools in resolving conservation issues complicated by hybridization. Hybridization between threatened Northern Spotted Owls (*Strix occidentalis caurina*) and invasive Barred Owls (*S. varia*) occurs and viable offspring are produced (Hamer et al. 1994, Kelly and

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Forsman 2004). However, *Strix* hybrids that backcross with Spotted Owls produce fewer offspring, which potentially reduces their fitness (Haig et al. 2004, Kelly and Forsman 2004). Mitochondrial DNA and amplified fragment length polymorphism (AFLP) analyses have proved to be reliable methods for accurate identification of *Strix* hybrids (Haig et al. 2004). Additionally, Funk et al. (2007a) identified four diagnostic microsatellite loci that successfully differentiated F_1 hybrids from backcrosses where AFLP and field identification methods failed. These markers are useful to law-enforcement officials who must be able to discern between "take" of Spotted Owls and hybrids to effectively protect the Spotted Owl.

Genetic markers may also be useful in identifying site-specific management actions for removing hybrids. Hawaiian Ducks (*Anas wyvilliana*), or Koloa, are a Federal and State endangered species endemic to the Hawaiian islands and readily hybridize with introduced feral Mallards (*A. platyrhynchos*) (Fowler et al. 2009). Fowler et al. (2009) used AFLPs and microsatellites to distinguish between hybrids and Hawaiian Ducks and then to evaluate the relative contributions of Mallards and Hawaiian Ducks to the hybrids. They found differences in the contribution of hybrids on different islands, suggesting that island-specific management actions may be warranted. Finally, because they were able to effectively differentiate hybrids and Hawaiian Ducks using molecular tools, a morphological field key is being created and tested with molecular data to help guide hybrid-removal actions.

Levels of hybridization and introgression of the critically endangered New Zealand Black Stilt or Kaki (*Himantopus novaezelandiae*) with the self-introduced congener, the Pied Stilt or Poaka (*H. himantopus leucocephalus*), were documented using a Bayesian admixture analysis of microsatellite data with mitochondrial DNA sequence data (Steeves et al. 2010). From this analysis it was demonstrated that hybrids could be identified by plumage characteristics and that, despite extensive and bidirectional hybridization, there was almost no evidence for introgression from Poaka to Kaki, which is likely attributable to reduced reproductive success in female hybrids and a transient male-biased Kaki sex ratio. Such a finding was counter to popular beliefs and critical to deciding whether or not to promote hybridization to facilitate genetic rescue, or whether to prevent it.

Conservation prioritization.—Even after taxa are delineated, limited resources force biologists, managers, and policymakers to implement triage when allocating funds for conservation (Bottrill et al. 2008). Various taxonomy-based prioritization schemes have been proposed. For example, phylogenetic diversity measures may be used to prioritize biodiversity conservation based on evolutionary history, thereby affording increased protection to distinctive taxa (Vane-Wright et al. 1991, Faith 1992) at any level of taxonomic hierarchy (Avise 2000). Phylogenetic approaches to conservation are flexible and powerful, but they are dependent on phylogenetic hypotheses that are themselves works in progress and can sometimes change considerably when new data or methods of analysis become available. For example, the last three annual supplements to the *AOU Check-list of North American Birds* (Banks et al. 2008; Chesser et al. 2009, 2010) added four orders and 15 families to the previous list as a direct result of new studies on the avian tree of life (Hackett et al. 2008). Such changes greatly affect phylogenetic diversity measures when they result in long branches associated with higher taxa with few extant species, or even species that form monotypic families or genera. For example, in the New World, recent molecular studies have resulted in the erection or resurrection of monotypic families for the Osprey (Pandionidae: *Pandion haliaetus*), Magellanic Plover (Pluvianellidae: *Pluvianellus socialis*), Sharpbill (Oxyruncidae: *Oxyruncus cristatus*), and Black-capped Donacobius (Donacobiidae: *Donacobius atricapilla*) (Remsen et al. 2010). Diversity in the order Ciconiiformes has been reduced from 117 to 19 species with the transfer of Ardeidae, Scopidae, Balaenicipitidae, and Threskiornithidae to the Pelecaniformes (Chesser et al. 2010). Similarly, phylogenetic analysis of molecular data sets of New Zealand "honeyeaters" showed that the rare Stitchbird (*Notiomystis cincta*), extirpated from North Island and numbering fewer than 2,000 individuals on an offshore island, represents a monotypic family (Notiomystidae) with a divergence of 34 million years ago (Ma) from its closest relatives, the New Zealand Wattlebirds (Callaeidae; Driskell et al. 2007). The Hawaiian Honeycreepers (Mohoidae) are a similar case: all four species were lost before they were identified to science (Fleischer et al. 2008). If a goal of conservation is to preserve as much of the tree of life as possible, consideration should be given to protecting regions that harbor these highly divergent taxa. Molecular data can often provide a clear window into the true structure of that tree.

POPULATION STRUCTURE

Development of microsatellite markers in the 1990s revolutionized our ability to understand population structure in birds. New sequencing technology has exponentially increased this capability (inset 1; Lerner and Fleischer 2010). Further, comparing microsatellite results with mitochondrial sequence data juxtaposes recent population processes with changes in population structure over evolutionary time. Thus, detailed estimates of genetic diversity, population structure, effective population size, and gene flow are now possible and robust where previously such estimates were problematic in bird studies.

Consideration of demographic information with genetic data further strengthens our understanding of detailed population structure. Funk et al. (2010) used this approach to identify recent population bottlenecks for Northern Spotted Owls (*Strix occidentalis caurina*) and found that genetic results were correlated with long-term demographic trends from the same sites. A severe ancient bottleneck was also detected in the British Golden Eagle (*Aquila chrysaetos*), although in this case the bottleneck did not appear to affect demographic stability (Bourke et al. 2010). Conversely, Brekke et al. (2010) found severe inbreeding depression among a reintroduced population of the endangered Hihi (*Notiomystis cincta*) in New Zealand.

Integration of ancient DNA (inset 3) into analyses of population structure can provide a more direct view of historical population structure and identify otherwise cryptic phylogeographic patterns. For example, using ancient mtDNA from bones preserved in lava tube caves, Paxinos et al. (2002) found a previously unknown radiation of geese in the Hawaiian archipelago associated with the independent evolution of flightlessness and gigantism on different islands.

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ANCIENT DNA

The discovery that DNA survives in (and can be amplified from) museum and archeological specimens has enabled considerable progress in avian conservation studies (Fig. 3; Wayne et al. 1999, Willerslev and Cooper 2005, Lee and Prys-Jones 2008, Rawlence et al. 2009). Use of ancient DNA (aDNA) provides a means to address issues in all the major subdisciplines of taxonomy and population genetics that benefit from a direct historical perspective. Although initially limited to studies of mtDNA, recent advances in primer design now permit sexing of museum specimens and phylogenetic reconstructions using ancient nuclear DNA for some taxonomic groups (Huynen et al. 2003, Irestedt et al. 2006, Bantock et al. 2008, Lambert et al. 2009). Thus, using ancient mitochondrial and nuclear DNA, we can elucidate the tempo and mode of evolution (Lambert et al. 2002, Ritchie et al. 2004, Baker et al. 2005), determine historical population sizes (Groombridge et al. 2009, Lambert et al. 2009), reconstruct cryptic population histories (Paxinos et al. 2002, Groombridge et al. 2009, Huynen et al. 2010, Peery et al. 2010), compare population histories with geological or anthropogenic events (Ritchie et al. 2004, Johnson et al. 2010, Peery et al. 2010), examine the evolutionary relationships of extant and extinct birds (Sorenson et al. 1999, Fleischer et al. 2000, Baker et al. 2005, Bunce et al. 2005), and evaluate hypotheses regarding extinction processes (Cooper et al. 1996, Allentoft et al. 2010).

Technical problems remain with extracting and amplifying aDNA and the resulting allelic dropout. The reliability and repeatability of demographic reconstructions based on aDNA have also been challenged by postmortem DNA instability (Binladen et al. 2006, Axelsson et al. 2008). However, methods for accommodating the effect of aDNA damage on inferences of demographic histories are available (Rambaut et al. 2009).

Ancient DNA can be obtained from a variety of avian tissues. To date, methods have been developed to amplify aDNA from bones (Lambert et al. 2002), museum skins (Mundy et al. 1997), feathers (Rawlence et al. 2009), eggs (Lee and Prys-Jones 2008), sediment deposits (Haile et al. 2007), and, most recently, prehistoric fossil eggshells (Oskam et al. 2010). The number of complete ancient mitochondrial genomes has increased rapidly with the advent of high-throughput sequencing techniques (inset 1; Ho and Gilbert 2010). Although amplification of the whole mitochondrial genome is now a reality, gains provided by increasing the amount of mitochondrial sequence data may be tempered by increased probabilities of contamination and failure (Lee and Prys-Jones 2008).

Fig. 3. (A) Jesse D'Elia (Oregon State University, U.S. Fish and Wildlife Service) at Eureka High School's Hall of Ornithology, taking a toe-pad sample from a California Condor (*Gymnogyps californianus*) that was collected in northern California in the late 1800s. Condors were extirpated from the Pacific Northwest ~100 years ago, and ancient DNA can provide insights into historical population size and structure, which may help inform future reintroduction strategies. (B) California Condor bones recovered from an archeological dig near The Dalles, Oregon (radiocarbon dates indicate that these bones may be 7,000–11,000 years old). Morphometric evidence suggests that condor bones from this site may represent an extinct condor species (*G. amplus*). Analysis of ancient DNA is providing an additional avenue of inquiry into their correct taxonomic placement.

Analyses of aDNA have shed light on previously unknown taxa and added to our knowledge of biodiversity and ecosystem function. Recently, aDNA was examined from the Bogotá Sunangel (*Heliangelus zusii*), known only from the holotype collected over 100 years ago and presumed extinct (IUCN 2010). Kirchman et al. (2010) used aDNA to show that the Bogotá Sunangel is a valid species and that it is more closely related to the high-elevation Gray-bellied Comet (*Taphrolesbia griseiventris*) and sylphs (*Aglaiocercus* spp.) than to low-elevation *Heliangelus* spp., which suggests that it may yet be found in isolated parts of the high Andes. Ancient DNA was also used to establish the validity of the Large-billed Reed Warbler (*Acrocephalus orinus*), known for 135 years from a single specimen collected in India in 1867 (Bensch and Pearson 2002). This revelation led to the discovery, also via aDNA, of 10 additional museum specimens of Large-billed Reed Warblers, previously misidentified as Blyth's Reed Warblers (*A. dumetorum*), and the Large-billed Warbler's subsequent rediscovery in Thailand (Round et al. 2007) and Afghanistan (Timmins et al. 2009). Methods based on aDNA were similarly used to examine the relationship between Ivory-billed Woodpeckers (*Campephilus principalis*) in the Americas. Fleischer et al. (2006) found that the Cuban subspecies (*C. p. bairdii*) was not the result of an introduction of *C. p. principalis* from the United States. Hence, loss of both taxa represents a more significant loss of biodiversity.

Population studies can benefit from aDNA approaches because incorporating modern and aDNA sequences into population reconstructions provides a better understanding of why the status of a population changed and what might be done to remedy a decline in effective population size (Ho 2007, Draheim et al. 2011). However, aDNA can be insufficient to accurately infer population histories, because reconstructions from modern data rely on extrapolations rather than direct observations of the fossil record (Wayne et al. 1999). This renders them biased toward reflecting recent or extreme events (e.g., recent population bottlenecks; Groombridge et al. 2009, Ramakrishnan and Hadly 2009, Peery et al. 2010). Thus, caution is warranted when interpreting results from aDNA studies that rely on specimens from a single period. Inclusion of aDNA across multiple periods may improve the reliability of historical population reconstructions (Ramakrishnan and Hadly 2009).

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Comparing results across taxa can also help illuminate small population processes. Evans and Sheldon (2008) analyzed microsatellite data from 194 bird species and found a significant decline in mean heterozygosity with increasing extinction risk. They suggested that smaller population sizes of threatened species were largely responsible for this relationship and that bird species at risk were relatively depauperate in terms of neutral genetic diversity.

Ultimately, results of conservation genetic efforts for populations are used in defining units for conservation. These discussions are often confusing because there are legal designations of populations under the ESA (i.e., DPSs; USFWS and National Marine Fisheries Service 1996) and there are overlapping terms used in the conservation literature to describe conservation units (e.g., Ryder 1986, Moritz 1994). Molecular markers can greatly aid both efforts, but distinctions between the two aspects of describing populations of concern must be understood. Often broken down into ESUs and management units (MUs), there are many ways to describe conservation units, but none of these have a legal basis for protection (Fraser and Bernatchez 2001). Conversely, DPSs carry legal protection for the areas and species identified. The USFWS has come to depend more and more on molecular evidence for ESA–DPS decisions as the costs of generating the data decline and the need for better quantification of population boundaries increases (Fallon 2007, Kelly 2010).

Small populations: Pedigree analyses.—Pedigree analyses, which combine direct observations, molecular markers, and pedigree models, have been underutilized in avian-conservation efforts for wild and captive populations (Haig and Ballou 2002, Kruuk and Hill 2008, Pemberton 2008). The paucity of microsatellites identified in bird studies (Primmer et al. 1997) prior to development of fast-throughput sequencing rendered this approach limiting for avian applications because there was not enough statistical power to differentiate among individuals, particularly closely related individuals. However, high-throughput sequencing technology now provides access to far more microsatellite markers and single-nucleotide polymorphisms (SNPs) for these important analyses (inset 1; Anderson and Garza 2006, Backström et al. 2006, Hauser et al. 2011). Field observations and sampling of many full families can also add confidence to molecular pedigree assessments; however, caution is warranted if the mating system is not well understood (Charmantier and Réale 2005, Wang and Santure 2009).

Despite these cautions, molecular pedigree assessments have yielded important information about reductions in effective population size in wild animals (Slate 2008, Sillanpää 2011). Townsend (2009) found disease-mediated inbreeding depression in a wild population of cooperative American Crows (*Corvus brachyrynchus*), and Ortego et al. (2007) identified the importance of understanding individual genetic diversity as it is related to clutch size and egg volume in small populations. Inbreeding avoidance or lack thereof has also been investigated in a number of studies (e.g., Keller and Waller 2002, Hansson et al. 2007, Grant and Grant 2008, Keller et al. 2008, Jamieson et al. 2009, Szulkin et al. 2009, Bush et al. 2010).

In principle, once molecular markers identify genetic relatedness among pedigree founders and confirm parentage, pedigree models use the subsequent pedigree to evaluate the current status of a population, investigate strategies for reintroduction or translocations, or predict potential changes in effective population size as a result of better pedigree or population management (Haig and Ballou 2002). Recently, pedigree analyses have proved helpful in developing management plans for maintaining genetic variation in free-ranging populations of the Takahē (*Porphyrio hochstetteri*), an endangered flightless New Zealand rail (Grueber and Jamieson 2008), and in White Storks (*Ciconia ciconia*) in Sweden (Olsson 2007).

Population connectivity and metapopulations.—A metapopulation is a group of spatially segregated, but demographically interacting ("connected"), populations. It is a useful concept for understanding avian population structure and dynamics, even in migratory species in which populations are not spatially discrete throughout the annual cycle (Esler 2000). However, not all fragmented populations behave as metapopulations; thus, genetic data can be used to infer a population's spatial organization (e.g., patchy populations, metapopulations, or isolated populations; Mayer et al. 2009). Estimating metapopulation connectivity or sex-biased dispersal patterns (recently reviewed for all taxa by Broquet and Petit 2009) is an important aspect of conservation genetics because it helps identify factors contributing to the decline of effective population size (i.e., species status). In the past, avian dispersal has been measured indirectly, via analysis of band returns (Crochet 1996), or via use of mitochondrial DNA or limited numbers of microsatellite markers. Thus, the chance of finding markers that track specific populations or individuals within them was considered quite slim, even if there was some degree of population differentiation. However, fast-throughput sequencing changes this paradigm and opens a new chapter in our ability to track birds at multiple temporal and spatial scales.

Regardless of the marker, many bird species, particularly migratory species, exhibit low levels of population genetic structure because their ability to fly makes them good dispersers (Crochet 1996). Thus, although habitat fragmentation has been a major focus in conservation biology, it has had little detectable effect on genetic structure in most recent avian studies (e.g., Brown et al. 2004, Funk et al. 2007b, Barnett et al. 2008, Draheim et al. 2010). Barnett et al. (2008) interpreted a lack of genetic structure among habitat fragments as evidence for ongoing gene flow. However, potential "time lags" between the onset of habitat fragmentation and their ramifications for population connectivity were not considered. Care is required when evaluating evidence for ongoing connectivity of populations, especially if the populations in question are not at migration–drift equilibrium (Crochet 1996). Segelbacher et al. (2003) addressed this problem by sampling populations with different levels of spatial discontinuity (i.e., continuous range, metapopulations, isolated populations) and temporal isolation (recent vs. long isolated) to determine how much genetic differentiation had accumulated. By contrast, nonmigratory bird species may exhibit high levels of differentiation and thus be more amenable to "traditional" studies of population structure. For instance, Galbusera et al. (2000) successfully used assignment tests with microsatellite loci to identify individuals descended from migrants in recently isolated populations of Taita Thrushes (*Turdus helleri*) and showed significant genetic differentiation between the only three remaining subpopulations.

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Recent reviews (Bossart and Prowell 1998, Lowe and Allendorf 2010) caution against making inferences about demographic connectivity solely from genetic data and recommend using telemetry or mark–recapture data to validate such conclusions. For instance, Fedy et al. (2008) employed genetic and telemetry methods to study connectivity among populations of White-tailed Ptarmigan (*Lagopus leucura*) and found that although genetic data suggested moderate gene flow between sites, telemetry data did not capture the movement of any individuals between populations. Mayer et al. (2009) used banding surveys in conjunction with nine microsatellite loci to quantify connectivity and identify which spatial model (patchy populations, metapopulation, isolated populations) best explained movement patterns of Reed Buntings (*Emberiza schoeniclus*). Rollins et al. (2009) used 11 microsatellite loci to study invasive European Starlings (*Sturnus vulgaris*) in Australia and were able to verify the source population of new invasions, validate the existence of a sex-biased dispersal system, and confirm that gene flow between subpopulations would make complete eradication of a population difficult, necessitating continual management. Similarly, Barrientos et al. (2009) used molecular markers to track movements of Trumpeter Finches (*Bucanetes githagineus*) throughout the annual cycle and across populations to document new population formation. They determined that movements of individuals toward sites outside their current range during the nonbreeding season are likely to precede the establishment of new breeding sites at the periphery of the distribution range. Conversely, Funk et al. (2007b) measured adequate gene flow among Great Basin and Pacific Coast Snowy Plovers (*Charadrius alexandrinus*), but banding information suggested quite minimal movement between these inland and coastal areas. As a result, a DPS was defined under the ESA on the basis of demographic isolation rather than genetics.

Dispersal abilities are particularly high among migratory birds, in which long-distance movements, high dispersal rates, and high rates of gene flow can minimize genetic differentiation of populations (Grinnell 1922, Wetmore 1926, Böhning-Gaese et al. 1998, Belliure et al. 2000 in Winker 2010b). This is particularly true in North America because repeated population isolation and expansion associated with Pleistocene climatic fluctuations has played an important role in structuring intraspecific genetic variation in northern temperate birds (Avise and Walker 1998, Klicka and Zink 1999, Milá et al. 2000, Klicka et al. 2011). This has resulted in low resolution when using standard approaches for measuring connectivity, such as estimating gene flow among populations or identifying individuals dispersed from other populations (called "migrants" in the population genetics literature) via population assignment tests.

In one of the first studies of avian population structure to use high-throughput sequencing, Li and Merilä (2010) identified 107 microsatellite markers across the Siberian Jay (*Perisoreus infaustus*) genome and used them to examine sex-biased dispersal. They estimated the scale at which linkage disequilibrium among markers decayed for each sex. Because (1) males had lower heterozygosity and (2) linkage disequilibrium decayed much faster for females, they concluded that dispersal is female biased (but did not estimate the geographic distances over which this occurred).

Several recent connectivity studies have gone beyond inferences based solely on genetic structure. Broquet et al. (2009) proposed a model to estimate direct migration rates by comparing genotypes of a population before and after dispersal. This model did not require migration–drift or Hardy-Weinberg equilibrium and was robust even when few microsatellite markers were available. However, it has not yet been applied to avian taxa and performs best when a high proportion of individuals from each population are sampled. Peery et al. (2008) used parentage assignments and demographic simulations to evaluate the role of immigration in sustaining a threatened population of Marbled Murrelets (*Brachyramphus marmoratus*). Microsatellite genotypes were used to estimate the number of parent–offspring pairs within the population compared to numbers expected under different models of immigration (i.e., a closed population versus a sink population). A related study compared historical and current genetic structure in those populations and found that migrants were significantly less likely than resident birds to be involved in parent–offspring pairs and, thus, unlikely to rescue the declining populations (Peery et al. 2010). By focusing on individuals rather than population genetic structure and not assuming equilibrium, such methods promise new insights into contemporary levels of connectivity (Palsbøll et al. 2010).

Genetic data can be used to infer whether the current spatial organization of populations reflects historical population structure or results from anthropogenic habitat fragmentation (inset 3; Segelbacher et al. 2003, Miller and Haig 2010). Moreover, if we can measure the effect of historical habitat connectivity or fragmentation on gene flow, we will be better equipped to make predictions regarding the effect of future climatic or habitat conditions on gene flow and population viability (Hoelzel 2010).

By linking demographic data with genetic data, cryptic population processes may emerge that are not evident when looking at these factors in isolation (Peery et al. 2010). Genetic identification of a new and distinct population of the secretive Black Rail (*Laterallus jamaicensis*) in the Sierra Nevada of northern California resulted in reconsideration of conservation priorities for the species (Girard et al. 2010). Incorporating genetics into metapopulation viability analyses may also allow one to assess the extent to which facilitating gene flow may slow the loss of heterozygosity and alleviate the projected effects of inbreeding depression (Pienkowski et al. 1998, Segelbacher and Storch 2002, Schiegg et al. 2006).

Metapopulation management: Translocations and reintroductions.—Translocations and reintroductions can be used to (1) supplement small or declining populations; (2) re-establish populations within their historical range; or (3) establish populations in novel areas (i.e., assisted migration and colonization) because their historical range is, or is likely to become, uninhabitable as a result of climate change, invasive species, habitat destruction, or a nexus of other threats. From a conservation genetics perspective, it is best to augment or re-establish metapopulations with individuals from populations that were connected historically by gene flow to reduce the chances of outbreeding depression and to increase the chances of retaining genomic components that reflect local adaptation (Storfer 1999; but see Jacobsen et al. 2008). Currently, evidence of avian outbreeding depression is scarce (Frankham et al.

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2010; but see Marr et al. 2002) and predicting the risk of its occurrence is one of the most important unmet scientific challenges in the field of conservation genetics (Frankham 2010). In small populations, reducing the risk of outbreeding depression must be balanced against the need to minimize inbreeding (Keller and Waller 2002) and manage genetic variation to facilitate long-term persistence of the source and target populations (Haig et al. 1993). In extreme circumstances (e.g., when a species would otherwise go extinct), intercrossing different but closely related taxa or ESUs (i.e., genetic rescue; Tallmon et al. 2004) may be the only method for preserving portions of an imperiled species' genome (Tarr and Fleischer 1999, Tallmon et al. 2004, Hedrick and Fredrickson 2010). In translocating individuals into small populations, one must always consider the potential for complete replacement of small gene pools by genetically more diverse individuals that may be more fit (i.e., genetic swamping; Bouzat et al. 2009). Thus, demographic challenges need to be addressed prior to genetic considerations (Frankham et al. 2010), and risk analysis of options is usually advisable.

Where there is significant uncertainty in the genetic makeup of source or donor populations for translocations, and where the effects may be irreversible, moving individuals can be tantamount to ecological gambling and counter to the precautionary principle in conservation biology (*sensu* Ricciardi and Simberloff 2009). Yet, in the crisis discipline of conservation biology, risk management requires that one weigh the risk of inaction against the risk of action. A genetic assessment of intra- and interpopulation differentiation prior to translocations can help quantify uncertainty and risk associated with artificially creating gene flow, evaluate the appropriateness of alternative population sources or targets (e.g., Haig et al. 1993; Tarr and Fleischer 1995, 1999), and set priorities for conservation of genetic diversity (Haig et al. 1990, Boessenkool et al. 2007).

Following implementation of translocations, genetic assessments can measure whether the movement of animals met genetic or demographic management goals. For example, Bouzat et al. (2009) found that translocations of Greater Prairie Chickens (*Tympanuchus cupido pinnatus*) were an effective tool in decreasing inbreeding coefficients and increasing genetic diversity while not swamping the genetic makeup of the target population. Conversely, translocations of New Zealand's South Island Robins (*Petroica australis australis*) to island refugia resulted in high levels of inbreeding, low levels of genetic diversity, and higher hatching failure rates, which suggests that future translocation efforts warranted more careful consideration of founder composition and numbers (Boessenkool et al. 2007). Talbot et al. (2003) discovered that translocation of Dusky Canada Geese (*Branta canadensis occidentalis*) to augment a population on Middleton Island in the Gulf of Alaska was not effective because subsequent population increases were determined to be the result of immigration from other islands rather than translocated geese. This finding would have gone undetected without an understanding of population structure from genetic markers. Finally, a severe population bottleneck suffered by captive White-headed Ducks (*Oxyura leucocephala*) led Muñoz-Fuentes et al. (2008) to recommend that more genetically diverse populations be established in captivity and the wild.

Migratory connectivity.—Migratory connectivity is the geographic linking of individuals or populations between stages of a life cycle or throughout an animal's life cycle (Webster et al. 2002, Marra et al. 2006; see www.migratoryconnectivityproject.org). Long seasonal migrations of many temperate bird species confound some of the traditional interpretations of connectivity applied to other taxa, in which it is primarily defined as movements between "suitable patches" that serve as year-round or breeding habitat (Hilty et al. 2006). By contrast, migratory birds may aggregate differently in winter and breeding habitats, with potential for genetic structure depending on whether pairing occurs during migration or on the breeding grounds (Flint et al. 2009, Winker 2010b). Genetic approaches to investigating migratory connectivity have been most effective when integrated with banding surveys, satellite telemetry, and isotope analysis (e.g., Clegg et al. 2003, Hobson 2005, Kelly et al. 2005, Hellgren et al. 2008), although stock identification (matching individuals to breeding populations based on genetic assignment) at overwintering grounds has succeeded in some cases (Haig et al. 1997). For example, Sonsthagen et al. (2009) identified hierarchical spatial genetic structure in Common Eiders (*Somateria mollissima*) breeding along a migratory corridor. Likewise, Wenink et al. (1993) used mitochondrial DNA lineages of Dunlin (*Calidris alpina*) at winter sites to assign individuals to their population of origin. Pearce et al. (2000) used microsatellite genotypes and mitochondrial DNA from Canada Geese (*Branta canadensis*) collected at hunter check stations to determine how harvest was affecting similar-appearing subspecies or populations with different conservation status (i.e., declining or stable). Cadiou et al. (2004) attempted to assign breeding origin to Common Guillemots (*Uria aalge*) that died in a massive oil spill at their wintering grounds using microsatellite data. The characteristic limitation imposed by weak genetic structure prevented accurate genetic assignment, but Cadiou et al. (2004) concluded that the die-off was unlikely to cause loss of much genetic diversity, given that genetic structure was so weak. Flint et al. (2009) used the lack of genetic structure, in combination with banding returns, to determine that populations of Pintails (*Anas acuta*) in North America and Asia routinely exchange migrants in numbers irrelevant to demography but sufficient to allow gene flow and, perhaps, transmission of parasites.

On the other hand, Hall et al. (2009), in an extension of the novel approach employed by Peery et al. (2008), estimated the proportion of migrants at different seasons in a peripheral population of Marbled Murrelets using assignment tests from 13 microsatellite markers. They used simulations to determine threshold levels of significance for identifying migrants that balanced Type I and Type II error and estimated the reproductive contribution of those migrants by identifying possible parent–offspring pairs involving migrants and comparing those with expectations generated from demographic models. Despite low genetic structure between peripheral (central California) and source (Alaska) populations, which could have precluded direct estimation of migration rates from assignment tests, they concluded that most migrants were females and the population was composed of a high number of migrants in the winter, but few migrants were present during breeding seasons and there were few individuals of mixed ancestry. This approach required assumptions about the demographic history of the population but demonstrated a potential solution to the typical problem that assignment tests are most reliable for detecting migrants only when there is strong genetic structure (i.e., very low migration).

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Because avian migrations have important implications for the transmission of disease, recent studies have also used genetic information from parasites to illuminate interactions among host populations. Waldenström et al. (2002) sequenced mitochondrial DNA of hemosporidian parasites harbored by migratory songbirds and determined that some parasites were more likely acquired on African overwintering grounds than on European breeding grounds. Koehler et al. (2008) conducted phylogenetic analyses of avian influenza strains isolated from migratory Northern Pintails and concluded that transcontinental migration facilitated coinfection by, and reassortment of, multiple strains of influenza. Although those studies were more focused on determining the source of particular infections, other studies have attempted to identify breeding grounds on the basis of hemosporidian parasite assemblages in migratory birds (e.g., Fallon et al. 2006, Pagenkopp et al. 2008). However, these studies require highly differentiated, geographically distinct parasite lineages and have had limited success to date.

Finally, high-throughput sequencing and other high-resolution methods (e.g., microarrays) will increase our ability to find population-specific markers to track bird populations (inset 1). Even so, analyses will be more successful if only markers that differentiate or suggest population differentiation are used to search for migratory patterns. Often, all markers are used in assignment tests, which results in less than definitive patterns, although all variable markers will be informative if dispersal measures that rely on estimating kinship are employed.

LANDSCAPE GENETICS

Landscape genetics is a relatively new discipline that has gained tremendous popularity in recent years (Manel et al. 2003, Storfer et al. 2007). Landscape genetic approaches extend numerous conventional population genetic analyses in a manner that provides identification of the effects of landscape features and landscape heterogeneity on genetic diversity and structure patterns within or across species (Miller et al. 2010, Safner et al. 2011). In addition to having conservation implications and improving our understanding of evolutionary ecology, landscape genetic analyses can further be used to examine topics such as disease transmission across a landscape (Ekblom et al. 2007) and climate change (see below). A November 2010 search of the term "landscape genetics" using ISI's Web of Science revealed more than 250 papers since 2003 that claimed to deal with this topic (as either self-reported by authors' key words or as annotated by ISI's "keywords plus" feature). Storfer et al. (2010) identified 655 published studies that included at least one landscape-level variable when interpreting genetic structure patterns. Interestingly, fewer than 10 of these studies involved birds (A. Storfer pers. comm.).

Prospects for landscape genetic investigations in avian taxa.—Many, if not most, avian taxa have the ability to circumvent or rapidly traverse landscape features that may disrupt or influence genetic structure patterns in less vagile organisms. Superficially, this attribute suggests that birds are not necessarily useful model species for landscape genetic investigations. Despite this assertion, we suggest that prospects exist to perform meaningful landscape genetic analyses for many avian taxa. As a conceptual framework, we consider two geographic extremes: taxa that breed in high-latitude geographic regions and those that inhabit more equatorial or tropical locales.

High-latitude locales.—Most avian species that use high-latitude breeding areas migrate to lower latitudes during winter. The mobility of such taxa suggests that prospects for detecting interesting patterns of genetic structure across landscapes should be low. In these cases, if genetic investigations are performed, one of three possible outcomes may be observed: (1) complete panmixia (no genetic structure; e.g., Veit et al. 2005); (2) isolation-by-distance (i.e., significant correlations between geographic distance and genetic distances of breeding populations; e.g., Draheim et al. 2010); or (3) subspecies-level differences among groups of breeding populations, coupled with the potential for either panmixia or isolation-by-distance within each subspecies group (e.g., Miller et al. 2010). In the latter case, genetic structure across space may be more likely to result from geographic separation of populations rather than particular aspects of landscapes per se. Inevitably, the likelihood of each outcome depends on the degree of natal- and breeding-site fidelity demonstrated by the species under investigation. Furthermore, these patterns may be apparent only when breeding population samples encompass extremely large (e.g., continent-wide) spatial extents. Thus, landscape-level features will probably not have a tremendous influence on species that inhabit high latitudes.

Despite this assertion, several studies have successfully implemented landscape genetic concepts and approaches, indicating that exceptions to the three scenarios stated above can occur. For example, analyses of the Golden-cheeked Warbler (*Dendroica chrysoparia*) by Lindsay et al. (2008) identified significant associations between genetic structure patterns and variables that encompassed population connectivity, forest fragmentation, and the percentage of agricultural land between breeding populations in Texas. Although the Golden-cheeked Warbler is a migratory species, the patterns observed in that study may be attributable to highly specific breeding-habitat requirements, a low overall number of breeding adults, and short dispersal distances between natal sites or the previous year's breeding sites. Furthermore, patterns from *D. chrysoparia* contrast starkly with the absence of genetic structure in the Cerulean Warbler (*D. cerulea*; Veit et al. 2005), a congener that migrates over longer distances to breed throughout the more heavily forested regions of central and northeastern North America. Genetic structure in Wrentits (*Chamaea fasciata*) across habitat fragments isolated by urbanization in southern California was surprisingly strong and concordant with levels of structure found in other, less mobile, vertebrates (Delaney et al. 2011).

Among avian taxa that inhabit higher latitudes, galliforms may be the best candidates for landscape genetic investigations, because of their low dispersal compared with other avian taxa (Barrowclough et al. 2004; Oyler-McCance et al. 2005a, b; Spaulding et al. 2006; Fedy et al. 2008) and strong associations with specific habitat types in some species of grouse (Braun et al. 1977, 1993; Zwickel and Bendell 2005; Hoffman 2006). For example, landscape genetic analyses applied to Capercaillies (*Tetrao urogallus*; Braunisch et al. 2010) in the Black Forest of Germany revealed numerous loose correlations between genetic structure and land-cover variables, including forest habitat quantity, forest edges, agricultural lands, and roads.

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Equatorial and tropical locales.—At lower latitudes, most bird species are nonmigratory and demonstrate low dispersal tendencies and, sometimes, reduced flight capabilities (Wallace 1889, Janzen 1967, Moore et al. 2008, Kerr et al. 2009, Ibarra-Macias et al. 2011). Many of these species also demonstrate higher levels of genetic differentiation across geographic space than taxa from more temperate climates, despite often inhabiting smaller geographic ranges (Brown et al. 2004 and references therein, Francisco et al. 2007, Burney and Brumfield 2009). These patterns reflect the generalized "latitudinal biodiversity gradient," which occurs at the interspecific level (Stevens 1989), among subspecies (Martin and Tewksbury 2008), and even within individual populations (Wikelski et al. 2003). Latitudinal diversity gradients are increasingly being addressed with the use of molecular markers (e.g., Martin and McKay 2004), and the results suggest that molecular diversity may parallel taxonomic and phenotypic diversity. Explanations for latitudinal diversity gradients encompass a variety of factors, including (1) historical climatic oscillation (Dynesius and Jansson 2000), (2) temperature kinetics (Wikelski et al. 2003, Allen et al. 2006), and (3) the greater efficacy of rivers and mountains as barriers in the tropics than in temperate locales (Janzen 1967, Brumfield and Capparella 1996, Bates et al. 2004). Of these factors, the last will most likely have the greatest effect within species. Consequently, in addition to potentially observing panmixia, isolation-by-distance patterns, and subspecies-level differences at different spatial scales, we suggest that analyses of tropical and equatorial avian taxa will harbor greater prospects for identifying signatures of landscape attributes on genetic structure patterns.

Despite recent interest in landscape genetic approaches, relatively few studies have applied these concepts and techniques to tropical and equatorial bird species. That said, molecular markers have highlighted the effects of forest fragmentation in several cases (Bates 2000, 2002; Brown et al. 2004; Reding et al. 2010). The potential effect of deforestation in tropical systems is well established. However, human-induced forest fragmentation will, in most cases, result in relatively new sets of landscape features. Consequently, studies that include historical and current range patterns in analyses (e.g., Pavlacky et al. 2009, Reding et al. 2010) may not only shed light on the genetic consequences of fragmentation itself, but also provide unique opportunities to discern the time scales over which the effects of such perturbations become detectable within natural populations.

Why perform landscape genetic investigations?—Given the growing application of landscape genetic approaches, we anticipate that there likely will be an appreciable increase in the number of such studies performed on avian species in the near future. As with all landscape genetic investigations, these efforts will provide more detailed insights into the factors that influence genetic diversity and structure at different spatial scales. We suggest numerous additional benefits, including identification of cryptic species, ESUs, subspecies, etc., that help prioritize important habitat for conservation. Of particular importance will be the identification of habitat types that can help promote connectivity and minimize population fragmentation (Braunisch et al. 2010). These insights may be enhanced if composite patterns from multiple species are considered simultaneously, because such efforts may help prioritize habitat requirements for entire suites of taxa within a geographic region (Vandergast et al. 2008, Miller and Haig 2010).

Outcomes from landscape genetic investigations may advance evolutionary ecology theory and promote development of new hypotheses. For example, identification of associations between landscape characteristics and patterns of genetic structure should generate hypotheses to explain the occurrence of such associations. We know, for example, that limited dispersal across tropical mountains or large rivers can create substantial spatial genetic structure (Capparella 1991, Brumfield and Capparella 1996) and that different species have varying abilities to move across some habitats (Moore et al. 2008, Ibarra-Macias et al. 2011). Those patterns lead to questions about what inhibits movements of some taxa across geographic space (i.e., neophobia) while not limiting movement of other taxa (Stratford and Robinson 2005, Burney and Brumfield 2009). Identification of ecological characteristics associated with limited movement can predict levels of genetic structure, even without extensive genetic data, and can help identify taxa that are likely to be sensitive to the effects of isolation, for example that resulting from forest fragmentation (Stratford and Robinson 2005). A wide variety of interesting behavioral or physical mechanisms could account for limited movements and may result from lower visual acuity of forest birds entering pasture or grassland habitats, limited physiological capacity for sustained flight, behavioral aversion to open habitats because of perceived predation risk, or even limited plasticity of physiological capacity when moving through unusual habitats (Harris and Reed 2002, Stratford and Robinson 2005).

Finally, because landscape genetic studies provide insights toward the degree of population connectivity and factors that promote it, results can help develop a better understanding of the dynamics of disease vectors and the spread of human and avian diseases (Archie et al. 2008). The classic example of this is the spread and effect of malaria on the birds of Hawaii (e.g., Beadell et al. 2006, Foster et al. 2007, Eggert et al. 2008, Jarvi et al. 2009). The introduced Southern House Mosquito (*Culex quinquefasciatus*) is the principal vector of avian malaria (*Plasmodium relictum*; Fonseca et al. 2006). Endemic birds of Hawaii have variable and relatively low resistance to this introduced malaria (van Riper 1986, Atkinson and Samuel 2010), although for most non-native species it is relatively benign. Currently, this mosquito occurs at or below 1,000 m, and nearly all native Hawaiian bird species that once occurred at or below this elevation no longer do. As the mosquito moves to higher elevations because of climate change, introgression from more cold-tolerant mosquito species, or both (Fonseca et al. 2006), more species will likely become exposed to this disease (Atkinson and Samuel 2010, State of the Birds 2010). Genetic sampling of mosquitoes across landscapes of varying elevations could provide a key to the location and direction of expansion of infected mosquitoes (Fonseca et al. 2000, Keyghobadi et al. 2006).

EMERGING APPLICATIONS

Climate change.—Measuring, predicting, and planning to mitigate the effects of climate change on wildlife species is of paramount importance (Intergovernmental Panel on Climate Change 2007). Fortunately, there are a number of genetic approaches that can offer direct and indirect contributions to this aspect of avian conservation. A directionally changing environment capable of producing massive demographic shifts is also capable of producing

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a massive selection event (Skelly et al. 2007). Although the rapid phenotypic and behavioral changes we are witnessing may be a function, in many cases, of phenotypic plasticity rather than adaptive evolution (Gienapp et al. 2008), there are growing examples of rapid adaptive evolution in response to climate change in birds (reviewed in Sheldon 2010). In a selection experiment with Blackcaps (*Sylvia atricapilla*), Pulido and Berthold (2010) demonstrated that nonmigratory Blackcaps were found in a completely migratory population after only two generations of directional selection for lower migratory activity. The strong evolutionary reduction in migration distance found in that study is in line with the expected adaptive changes in bird migration in response to environmental alterations caused by climate change (Bradshaw and Holzapfel 2006, 2008).

Molecular markers that track genetic patterns across populations or landscapes can help predict future rates of genetic changes in modified landscapes. One might predict that species (lineages) with higher genetic diversity would respond more rapidly to environmental variations along "leading" edges of ranges as climate changes. For example, climate predictions for the Pyrenees Mountains of Western Europe include further fragmentation of the "sky island" alpine habitat used by Rock Ptarmigan (*Lagopus muta*). Beck et al. (2009) discovered genetically isolated and depauperate populations that may need translocation if current habitat fragmentation continues. A multispecies study currently underway examines the effects of climate change on wetlands and waterbirds in the Great Basin (S. M. Haig et al. unpubl. data). Genetic structuring in highly vagile waterbird populations across this region is not strong enough to use molecular markers to monitor changes over a short time frame, but examining how ecological shifts across the landscape may affect the distribution, dispersal, and genetics of their aquatic prey species can be informative.

Despite advances in many areas of genetics, the potential for evolutionary responses is rarely considered in bioclimatic models of species' range shifts (Pearson and Dawson 2003, Skelly et al. 2007), even though such models are among the primary tools being used to assess potential effects of climate change on species distributions (e.g., Stralberg et al. 2009). Assuming that there will be no evolutionary response to climate change may result in overly pessimistic predictions, especially for species that disperse long distances, are under selection at range margins, or have short generation times that facilitate more rapid intergenerational selection. Therefore, the most appropriate application of predictive bioclimatic envelope models may be for long-lived species that are poor dispersers (Pearson and Dawson 2003), although Tingley et al. (2009) found that 90% of bird distributions resurveyed after 100 years in the Sierra Nevada of California indicated changes in their climatic niches. Development of more mechanistic models that incorporate the potential for an evolutionary response and predict evolutionary responses in tandem with ecological responses may provide additional realism and improve predictive strength (Skelly et al. 2007, La Sorte and Jetz 2010); however, doing so will require that we develop better molecular tools for measuring a species' potential for adaptive variation in novel environments (Scoble and Lowe 2010). Recent technological advances in genomics allow for not only the expansion of the amount of the genome examined but also the detection and characterization of functional genes that are responsible for survival and adaptation in such cases. This knowledge could help managers determine which species could be at greater risk or those that might be more likely to succeed using approaches such as translocations or reintroductions.

Ecotoxicology.—Ecotoxicological research has linked a broad taxonomic spectrum of avian population declines with exposure to numerous classes of contaminants, including (but not limited to) DDT and other organochlorine compounds (Ratcliffe 1967), mercury (Burgess and Meyer 2008), lead (Meretsky et al. 2000), selenium (Ohlendorf and Hothem 1995), agricultural pesticides (Goldstein et al. 1999, Mora 2010), and polycyclic aromatic hydrocarbons (Iverson and Esler 2010). Although the mitigation of exposure sources subsequently facilitated recoveries in some cases, the potential long-term effects on population structure, particularly population bottlenecks, are unclear. Modern genetic techniques (as described throughout this review) offer powerful tools to quantify a range of effects related to contaminant exposure and identify groups of birds that may face substantial risk of deleterious effects.

Although originally focused on narrow, single-species studies and overt symptoms of toxicity resulting from ecologically irrelevant exposures, the field of ecotoxicology has experienced a renaissance in developing a broader, more integrated understanding of the direct and indirect effects of contaminants on ecosystem function that span molecular to ecosystem scales of biological organization (Snape et al. 2004, Newman and Clements 2008). Yet despite these advantages, applications of genetic techniques to population- or landscape-scale ecotoxicological issues has lagged far behind other disciplines traditionally addressed in conservation genetics. Furthermore, avian taxa have been relatively neglected with respect to conservation genetic approaches to contaminant effects in comparison with other taxonomic groups, such as fish, amphibians, and invertebrates. The specific reasons for these research patterns are unclear but are likely attributable in part to the reductionist history of ecotoxicology (focus on mechanisms of damage as opposed to emergent effects of exposure) as well as the seeming intractability of linking contaminant exposure with latent responses in avian population genetic structure, particularly in the face of numerous other influencing factors related to avian vagility. However, substantial progress could be made in our understanding of how long-term contaminant exposure may influence population-level processes in wild birds by merging many of the conservation genetic approaches described throughout this review with a robust assessment of contaminant exposure at various life stages within an evolutionary toxicology framework (Staton et al. 2001).

Contaminants can influence individual and population genetic structure by directly damaging genetic material (Skarphedinsdottir et al. 2010) or through selective effects of chemicals on gene frequencies within exposed populations (Theodorakis et al. 2006). It is the latter effect to which conservation genetic approaches are most aptly applied. Because individuals often vary in their sensitivity to various contaminants, chronic exposure may result in fitness costs (e.g., reduced survival, impaired reproduction, or compromised immune response; Belfiore and Anderson 2001) in sensitive individuals. Thus, one would expect to see directional selection for tolerant genotypes if such susceptibility had a genetic basis. Unfortunately, attributing these types of responses to contaminant exposure among avian populations is exceedingly difficult because of their relatively long life spans and high dispersal abilities.

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Contaminant exposure may reduce overall genetic diversity within populations by reducing the effective population size, especially if barriers to gene flow exist (Evenden and Depledge 1997). Possible approaches for evaluating these potential effects require a general understanding of background population genetic structure and comparisons of genetic diversity between numerous exposed and unexposed populations or along gradients of exposure. Whitehead et al. (2003) employed this approach using AFLP and microsatellite markers in native fish species to test whether patterns of genetic variation were consistent with long-term pesticide exposure or with expectations based on biogeography. Agricultural systems are particularly promising areas in which to apply these approaches because they support a broad range of avian taxa, regularly receive generous doses of various herbicides and insecticides, and can often be studied with suitable replication. However, assessing population-level risk from exposures on the basis of genetic diversity may be the most promising application of conservation genetic tools to contaminant research. Small, isolated populations that already have low genetic variability are likely to be more vulnerable to external stressors such as toxic compounds, particularly if coupled with other barriers to gene flow. Integrating contaminant exposure research with assessments of genetic structure can help prioritize management efforts to preferentially reduce exposure in those populations that are least likely to have the genetic capacity to deal with chemical stressors.

Application of other emerging genetic tools, such as microarrays (Lettieri 2006), will help further our understanding of the mechanisms of contaminant effects. A deeper insight into how various classes of contaminants induce or alter gene expression and the associated phenotypic responses will provide better understanding of individual-level effects, identify species-specific sensitivity profiles, and help develop effective biomarkers of both exposure and effects. These approaches are now relatively common among fish, amphibian, and invertebrate taxa and merely await application to avian species.

The abundance of published avian conservation genetic and avian ecotoxicology studies highlights the importance of these two disciplines. Yet the dearth of current research linking them suggests the existence of a critical information gap and a clear area for research merging these issues. A logical starting point is to pair comparisons of genetic diversity among populations with a range of tissue contaminants in order to build data sets that can be used to test some of these hypotheses. Species with broad monitoring networks to build upon (e.g., Tree Swallows [*Tachycineta bicolor*], Wood Ducks [*Aix sponsa*], and Purple Martins [*Progne subis*]) may be particularly useful for these initial efforts. However, careful study design is imperative to sufficiently address other drivers of fitness or genetic diversity and minimize the potential for spurious results.

PERSPECTIVE

Molecular technology continues to evolve at an ever increasing pace. Recent development of high-throughput DNA sequencing has revolutionized our ability to examine hundreds of thousands of variable markers, whereas less than 5 years ago, avian geneticists were content with analyzing 5 to 10 variable microsatellite loci. Furthermore, over the past two decades, developments in examining ancient DNA have opened a completely new window into examining avian evolutionary and demographic history. The near future promises that an understanding of the complete genome of an individual or individuals across space and time will provide a deeper understanding of issues related to the effects of disease, toxins, population bottlenecks, and other processes on species, populations, and landscapes. The challenge for avian conservation geneticists is to understand how this new technology can be applied to answering critical questions related to avian conservation. We offer the following insights and perspectives for moving forward.

(1) Taxonomy is critical to conservation because it defines elements of biodiversity. Since its inception as a field of study, genetics has played a critical role in identifying and grouping taxa, and we expect that this role will continue to expand with advances in genomics. However, philosophical differences regarding how to recognize and define species, subspecies, and appropriate population units for conservation need to be resolved.

(2) Traditional genetic tools have been, and continue to be, successfully applied to a host of avian conservation issues, including improved assessment of population structure, gene flow, and pedigrees. Genomic approaches like the use of SNPs are likely to increase the discriminative power of these analyses by orders of magnitude, but a new wave of bioinformatic approaches will likely be necessary to handle the coming deluge of genetic information.

(3) Multiple data sets should be used to define taxa and population structure. These temporal and scalar comparisons can be key to understanding what type of conservation action is warranted.

(4) Incorporation of historical specimens (e.g., museum skins and subfossils) into genetic studies has revolutionized all major subdisciplines of taxonomy and population genetics that benefit from a direct historical perspective.

(5) Molecular markers can identify cryptic species and population processes that cannot be observed in any other way. Thus, they warrant consideration in most conservation investigations.

(6) The emerging field of landscape genetics can play a critical role in determining the effects of past, present, and future climatic and land-use changes on species and their populations.

(7) Ecotoxicological and genetic approaches to studying contaminant issues have yet to be widely integrated into avian studies but could prove insightful.

Ultimately, biodiversity conservation requires preservation of as much variation as possible at all taxonomic levels. To realize that goal, conservationists and geneticists need to maintain open lines of communication to design and implement strategies to help the world's marvelously rich assemblage of birds endure the current and future state of biodiversity triage.

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