



THE USE OF MOLECULAR MARKERS IN WILD TURKEY MANAGEMENT

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Abstract: A variety of genetic markers now are available for use in the management and conservation of wildlife species. In the wild turkey (*Meleagris gallopavo*), these markers have been used to address questions at levels ranging from the individual to the subspecies, and with issues ranging from species-wide evolution to forensics. Genetic studies involving translocated populations have provided managers with additional information to consider when designing optimal translocation strategies to maximize growth and long-term stability of such populations. In this paper, we discuss the molecular markers available for wild turkeys, and review their applications in wild turkey management, including subspecies identification, intraspecific hybridization, domestic introgression, genetic bottlenecks, population structure, gene flow, cryptic behavioral and social patterns, and forensics.

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Genetic markers have become a standard tool in the management and conservation of wildlife species, enabling scientists to address wildlife management questions at levels of biological resolution that previously had been unattainable with traditional techniques. When integrated with information from disciplines such as ecology, morphology, or paleontology, genetic data allow us to better understand evolutionary and demographic phenomena such as population structure (Sarre 1995, Sinclair et al. 1996, Kyle et al. 2000), dispersal rates (Beheler 2001, Richardson et al. 2002, van Hooft et al. 2003, Zenger et al. 2003), population bottlenecks and range expansion (Rogers and Harpending 1992, Rogers 1995, Luikart et al. 1998), cryptic behavioral and social patterns (van Staaden et al. 1996, DeWoody et al. 1998, Piertney et al. 1999, Zenuto et al. 1999, Storz et al. 2001), parentage (DeWoody et al. 2000, Beheler et al. 2003, Carew et al. 2003, Sinclair et al. 2003, Stapley et al. 2003), hybridization (Adams et al. 2003), taxonomic status (Miththapala et al. 1996, Stephen et al. 2005a), and individual identity (Cronin 1991, Guglich et al. 1994, Boyd et al. 2001, Manel et al. 2002). It has become apparent that the tools of modern molecular biology hold great value for the field of wildlife management.

However, it also is clear that the selection of the most appropriate class of genetic markers, both in terms of inheritance patterns and rates of evolution, is important if these tools are to be applied successfully at varying scales of biological organization.

In the wild turkey, a number of different types of molecular markers have been developed. These tools have been used in a variety of different applications to address management-oriented concerns at scales ranging from the subspecies to the flock. Molecular markers also have been used to investigate evolutionary relationships among subspecies and populations. In this paper, we will provide a brief review of the molecular tools that are available for use in wild turkeys, and summarize the management-related research that has been or is being conducted using these tools.

MOLECULAR MARKERS AVAILABLE FOR WILD TURKEYS

Allozymes

Allozymes are alternate (allelic) forms of nuclear DNA-encoded enzymes. Mutations in the DNA se-

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quence coding for an enzyme can induce changes in its protein structure. These differences in protein structure are detectable by starch-gel electrophoresis, which separates the enzyme alleles based on size, shape, and electrical charge. Early studies of allozyme variation among populations, beginning with a series of papers in 1966, revealed a surprising amount of genetic variability in natural populations (Harris 1966, Hubby and Lewontin 1966, Johnson et al. 1966). Allozyme markers have proven to be useful for applications ranging from characterizing broad-scale variation across a species range to investigating local mating patterns (Rhodes et al. 1993, Pope 1998, Lode 2001, Gabor and Nice 2004). Analysis of allozyme markers is relatively inexpensive, and the markers are codominant, meaning that all variants at a locus can be visualized. However, the utility of allozyme markers is limited by low levels of polymorphism, resulting from the fact that allozyme analysis detects only a subset of the total variation (that which affects the migration of the enzyme through a gel). Most enzymes are not polymorphic (e.g., average of 23% polymorphism for 551 species of vertebrates), and polymorphic loci rarely have more than 3 alleles (Nevo et al. 1983). Thus, the relatively low expense and ease of data collection often are offset by the large number of allozyme loci typically needed to adequately assess genetic variability in a sample. Additionally, because allozymes are expressed genes, they are subject to selection, and patterns of population variation may not always reflect the neutral processes assumed to drive divergence and gene flow (Eanes 1999).

Twenty-eight allozyme loci have been optimized for surveys of genetic diversity in wild turkeys (Stangel et al. 1992). Although subsequent studies screened all 28 loci, they typically found only 4–5 loci that exhibited polymorphism among the groups of interest (Leberg 1991, Leberg et al. 1994, Rhodes et al. 1995, Boone and Rhodes 1996). Although turkeys exhibit slightly fewer polymorphic loci than the average for vertebrate species, they are well within the range of values described for bird species (Nevo et al. 1983). Despite reduced genetic variability in comparison to DNA-based markers, allozymes are still valuable tools for subspecies- and population-level applications in the wild turkey (Leberg 1991, Stangel et al. 1992, Leberg et al. 1994, Rhodes et al. 1995, Boone and Rhodes 1996).

DNA-based Markers

Nuclear DNA

In recent decades we have witnessed a shift from protein-based (allozyme) to DNA-based marker systems for estimation of genetic parameters in wildlife species. DNA-based markers not only reveal more genetic variation than their allozyme predecessors, but also allow investigators to choose among sets of loci with different patterns of inheritance (nuclear versus mitochondrial DNA) or evolutionary constraints (coding versus noncoding regions of the genome; Mitton

1994). Nuclear loci represent DNA inherited from both parents, and therefore can be useful for questions focused at almost any biological scale, from establishing relatedness among individuals to discernment of species (Sinclair et al. 2003, Verma and Singh 2003, Williams et al. 2003a). In particular, highly polymorphic nuclear markers, often associated with noncoding regions of the genome, are essential for studies in which individuals must be unambiguously identified (i.e., parentage studies or assignment of unknown individuals to a population of origin; Anderson et al. 2002, Manel et al. 2002, DeYoung et al. 2003). However, the abundant polymorphisms that make highly variable nuclear markers attractive for applications at the individual level can, in some cases, obscure patterns of differentiation at higher taxonomic levels (e.g., species; Hedrick 1999).

Microsatellites.—Nuclear microsatellites are short segments of noncoding DNA (typically 2–4 base pairs in length) which are tandemly repeated many times. Microsatellite loci tend to mutate by adding and subtracting these segments, so allelic variation is generally in the form of length, which is easily detectable using electrophoresis. Microsatellite length polymorphisms can be abundant within and among populations, and it is thought that slippage during DNA replication plays a major role in generating length variation among alleles (Levinson and Gutman 1987, Jeffreys et al. 1991, Schlötterer and Tautz 1992). Suites of highly polymorphic microsatellite loci can provide tremendous discriminatory power, allowing for the unique identification of individuals within populations and the exclusion of individuals as potential parents of offspring. The highly polymorphic nature of microsatellite loci also means that they can be prone to a phenomenon termed homoplasy, where convergent mutations in different lineages have led to the same allele. Thus, alleles that are alike may not represent common ancestry, resulting in inferred relationships among groups that may not accurately represent evolutionary histories. The potentially confounding effects of homoplasy often can be alleviated by analyzing many microsatellite loci.

Microsatellite markers are relatively inexpensive to analyze, and are available for countless species in virtually every major taxonomic group. Furthermore, microsatellites developed for one species often can be used in related taxa (Frankham et al. 2002), further reducing the time and expense of their development for newly studied species.

Currently, 24 microsatellite loci have been optimized for use in wild turkeys. Eighteen of these loci originally were developed for domestic turkeys (Donoghue et al. 1999, Huang et al. 1999, Reed et al. 2000), but proved to be polymorphic in wild turkeys with modifications (Shen 1999, Latch 2004). The remaining 6 loci were developed by screening microsatellite repeats found in wild and domestic turkey DNA sequences (Latch et al. 2002). Robust subsets of these 24 loci have been used for numerous studies of wild turkey ecology and taxonomy (Mock et al. 2001, 2002,

2004; Latch 2004; Krakauer 2005; Latch and Rhodes 2005, 2006; Latch et al. 2006a,b). Numerous additional microsatellite loci have been developed for domestic turkeys but have not been thoroughly screened for polymorphism in wild turkeys (e.g., Reed et al. 2000, 2002, 2003). Given the previous success of domestic turkey markers in their wild relatives (Shen 1999, Latch 2004, Krakauer 2005), this represents a potential reservoir of microsatellite loci for future applications. In the wild turkey, the utility of nuclear microsatellites has been shown for elucidating genetic structure among turkey populations and identifying individual animals (i.e., Latch and Rhodes 2005, Latch et al. 2006b).

Amplified Fragment Length Polymorphisms (AFLPs).—Amplified fragment length polymorphism (AFLP) is another type of nuclear DNA-based marker system available for rapid screening of genetic diversity among individuals (Vos et al. 1995, Mueller and Wolfenbarger 1999). AFLP polymorphisms result from differences in restriction fragment lengths caused by single base mutations, insertions, or deletions that create or destroy restriction enzyme recognition sites. AFLP methods involve the detection of these sites by polymerase chain reaction (PCR) amplification and electrophoresis. Because AFLP methods can generate hundreds of genome-wide polymorphic markers without any prior sequence knowledge, AFLPs can be a powerful, low-cost tool for use in systematics and population genetics, as well as for generating “DNA fingerprints” for individual identification and studies of kinship (Escaravage et al. 1998, Mueller and Wolfenbarger 1999, Whitehead et al. 2003). The primary limitation associated with AFLP markers is that they are a dominant marker system, requiring the assumption of Hardy-Weinberg equilibrium for the estimation of allele frequencies in populations. In addition, AFLP profiles can be sensitive to varying laboratory conditions, rendering them difficult to replicate over long periods of time in different laboratories.

AFLP protocols have been optimized in wild turkey, and these markers have been used effectively to resolve evolutionary relationships among subspecies and to determine the subspecies of origin of a given population (Mock et al. 2001, 2002). Because of the large number of polymorphic AFLP loci in wild turkey, this marker system may also prove to be informative for fine-scale questions at the population, flock, or individual level.

Mitochondrial DNA

In contrast to the nuclear genome, mitochondrial DNA (mtDNA) is cytoplasmically inherited, and thus is derived almost exclusively from maternal lineages. Although the mtDNA of any individual can be unique, the highly conserved nature of homologous functional genes across a wide variety of organisms allows for direct comparisons of mtDNA sequences at many different taxonomic scales. Thus, mitochondrial markers, particularly those representing coding regions of the genome, are particularly valuable for questions per-

taining to higher level systematics and phylogenetics (Saetre et al. 2001, Abbott and Double 2003). Because mitochondrial sequences are generally nonrecombining, molecular clocks can be used to estimate divergence times of various taxa. In addition, because of their mode of inheritance, mitochondrial markers associated with maternal lineages are also useful for questions focused on population establishment, social structure, and hybridization (Zink and Dittmann 1993, Pilgrim et al. 1998, Boyce et al. 1999, Adams et al. 2003). However, despite relatively high levels of polymorphism at certain hypervariable regions of the mitochondrial genome, mtDNA markers may not possess sufficient variability for individual identification. This low variability can be a major limitation for the use of mtDNA markers in population-level studies.

Control Region.—The most variable portions in the mitochondrial genome are within the control region (D-loop), a noncoding region. Control region sequences frequently are the mitochondrial marker of choice for assessing patterns of genetic differentiation below the species level. In many investigations, nuclear markers are combined with control region data to characterize differences in patterns of genetic differentiation between the sexes (Scribner et al. 2001, Johnson et al. 2003, Zenger et al. 2003) and to provide a temporal framework for phylogenetic reconstruction. Two sets of PCR primers have been developed to amplify the control region in wild turkeys. One set amplifies a product of approximately 1,300 base pairs (Mock et al. 2001, 2002), and the other set amplifies a smaller product of about 500 base pairs (Latch 2004, Latch et al. 2006b). In wild turkeys, control region sequences exhibit substantial variability at the subspecies and population levels. Questions concerning sex-specific processes, such as sex-biased dispersal and introgression, will benefit from the use of maternally inherited markers such as the control region (e.g., Latch et al. 2006b).

Cytochrome b.—The mitochondrial cytochrome b gene is a relatively large mitochondrial gene that codes for a protein that has been well studied with respect to structure and function (Howell and Gilbert 1988, Tron et al. 1991, Crozier and Crozier 1992). This gene as a whole evolves relatively slowly and therefore is fairly conserved across taxonomic groups, although the third codon positions within the gene can show higher levels of polymorphism than first or second positions. Because of the conserved nature of this gene, sequence polymorphisms at the DNA and amino acid level often provide information at higher levels of biological organization (e.g., species, subspecies) than might be achieved for more rapidly evolving markers such as microsatellites. Although cytochrome b has most often been used to describe genetic relationships between subspecies, species, or genera, it may sometimes be suitable for analyses at lower levels of biological organization (i.e., among populations; Wenink et al. 1993). Cytochrome b DNA amplification and sequencing methods have been developed in wild turkeys, yielding high-quality sequence data from a 500

base pair portion of the cytochrome b gene (Latch 2004, Latch et al. 2006a). Although there is not a substantial amount of diversity in this region, pilot studies suggest that cytochrome b sequences may be practical for comparisons among eastern (eastern [*M. g. silvestris*], Florida [*M. g. osceola*], and Rio Grande [*M. g. intermedia*]) and western (Merriam's [*M. g. merriami*] and Gould's [*M. g. mexicanus*]) subspecies of the wild turkey (Latch 2004).

APPLICATIONS IN WILD TURKEY MANAGEMENT

Subspecies-level Applications

Subspecies Delineation in Naturally-occurring Populations

Subspecies are taxonomic units thought to represent evolutionary lineages below the species level. There is broad agreement among biologists that genetic variation below the species level could be important for the evolutionary flexibility of the species (Mitton and Grant 1984, Allendorf and Leary 1986). In the wild turkey, subspecies designations coincide with broad geographic/ecotypic regions and are presumed to represent units with some degree of common ancestry and local adaptation, which has been achieved over many thousands of years of evolutionary experience. Subspecies boundaries are an important management concept, because translocations of birds from one area to another may lead to the genetic "swamping" of locally adapted populations. Because translocation is one of the most widely used management practices for the wild turkey, understanding of historical relationships among subspecies is critical to the selection of appropriate source stock for translocations.

Mock et al. (2002) used a combination of DNA-based markers, both nuclear (AFLPs and microsatellites) and mitochondrial (control region DNA sequences), to characterize historical patterns of genetic diversity in relict wild turkey populations from each of the 5 recognized subspecies, and to assess the genetic validity of current subspecies designations (see range map available at http://www.nwtf.org/images/range_map_large.jpg or in Tapley et al. *this volume*). All 3 marker types showed less genetic diversity in the Gould's subspecies than in the other subspecies. Relationships among subspecies suggested by AFLP and control region data corroborated our understanding of historical habitat continuity. Microsatellite data suggested somewhat different evolutionary relationships among the subspecies. Mock et al. (2002) suggested that the relatively small number of microsatellite loci and the weak statistical support for the groupings may have led to the alternate pattern; however, adding 9 additional microsatellite loci and screening a subset of the samples used in Mock et al. (2002) did not change the inferred relationships among subspecies (Latch 2004). Differences in the evolutionary relationships among groups inferred by different marker systems are

not uncommon. Marker-related phenomena such as homoplasy can confound estimates of divergence times and relationships among groups, particularly at higher levels of biological organization. However, the inability of microsatellite markers to correctly resolve evolutionary relationships among wild turkey subspecies does not preclude their use at the subspecies level for classification purposes (see *Subspecies identification and hybridization in translocated populations* section below).

Latch (2004) performed a preliminary assessment of the utility of cytochrome b gene sequences for recreating the evolutionary relationships among wild turkey subspecies. These data indicate that although the differences between eastern (eastern, Florida, and Rio Grande) and western turkeys (Merriam's and Gould's) are substantial, the relatively slow rate of evolution within the cytochrome b gene has resulted in little or no structuring among subspecies within these broad regional groups.

Subspecies Identification and Hybridization in Translocated Populations

Although translocations have been a critical component of the successful restoration and expansion of wild turkey in North America (Kenamer and Kenamer 1996), the genetic implications of these translocations are poorly understood. Programs to reintroduce turkeys into previously occupied habitats, or to introduce them outside their historical range, often have not considered traditional species or subspecies ranges. Such programs threaten to disrupt historical patterns of genetic diversity and gene flow, which potentially could lead to irretrievable loss of genetic records of populations (Avisé 2004), increased homogenization of subspecies and the loss of unique, locally adapted forms, not to mention forced extinctions of native populations (Avisé 2004). Furthermore, some of these programs have led to situations in which multiple subspecies or variants now co-occur in regions where no such associations historically existed. Such situations have immediate implications for local hybridization between subspecies, and also mean that the best source stock for a translocation may no longer be that which is geographically closest. Before evolutionarily significant trajectories within the subspecies are completely eroded by human-mediated movements, it is important to understand their historical and contemporary distributions as well as the underlying genetic basis for differentiation among them.

DNA-based markers, including microsatellites, AFLPs, and mitochondrial control region sequences, can be used to determine the origin of an individual bird that has been translocated or that has migrated from one region to another (Paetkau et al. 1995, Ranala and Mountain 1997, Cornuet et al. 1999, Pritchard et al. 2000). Microsatellites are particularly promising for this application, because of their high level of polymorphism, their codominance, and the replicability of data within and among laboratories.

In southeastern Arizona, wild turkey managers

were concerned that efforts to reintroduce the Gould's subspecies into its historical range had been impeded by previous reintroductions of Merriam's turkeys into the area. Mock et al. (2001) used molecular markers to determine whether the turkeys currently inhabiting the Huachuca Mountains in southeastern Arizona were descended from the Gould's turkeys translocated there in the 1980s, or if interbreeding had occurred with descendants of Merriam's turkeys introduced to the area in 1950. Given the utility of these markers for distinguishing wild turkey subspecies (i.e., Mock et al. 2002), the authors used a combination of AFLPs, microsatellites, and control region sequences. They found that turkeys in the Huachuca Mountains consistently grouped with reference individuals from the Gould's subspecies (from Mexico) rather than with reference Merriam's turkeys from central Arizona (Mock et al. 2001). Thus, these data strongly indicated that the wild turkey population in the Huachuca Mountains was descended from the translocations of Gould's turkeys made in the 1980s, and showed no evidence of interbreeding with the Merriam's subspecies. Each of these 3 markers performed extremely well in this study, providing managers with several cost-efficient methods for distinguishing Merriam's and Gould's subspecies.

In Kansas, extensive translocation efforts have confounded subspecies distributions throughout the state. Today, 3 subspecies of wild turkey are believed to co-occur in Kansas—eastern, Rio Grande, and Merriam's. Given the likely disruption of historical subspecies structure within the state, and the inability of morphological methods to unambiguously resolve the subspecific status of turkeys, DNA-based methods were used to address these concerns. Microsatellites (Latch et al. 2006a) and control region and cytochrome b sequences (Latch 2004) were employed to characterize the genetic variability of wild turkey populations throughout Kansas, in an effort to clarify the current distribution of pure and mixed turkey subspecies. These molecular data were able to delineate subspecies boundaries and detect zones of hybridization between them. Furthermore, these data clearly indicated areas in which undocumented translocations significantly impacted the subspecific composition of turkeys in particular regions.

In the Davis Mountains of Texas and within nearby Rio Grande turkey populations, Latch et al. (2006b) assessed the subspecific status and degree of hybridization of individuals within an introduced population of Merriam's turkeys. Data from the Merriam's source population in New Mexico was used as a baseline reference for the genetic characteristics of the Merriam's subspecies. Nineteen years following the introduction event, microsatellite data indicated that the genetic integrity of the introduced population of Merriam's turkeys in the Davis Mountains Preserve has been eroded by both immigration from and hybridization with nearby Rio Grande populations. Data from the mitochondrial control region allowed for further characterization of parental contributions to hybrid individuals, and indicated that most hybrids were the result of im-

migrant Rio Grande males mating with resident Merriam's females.

Domestic Introgression

Early in the history of wild turkey translocation programs, managers considered the potential utility of game-farm or domestic turkeys as source stock for translocations into the wild. One concern was that the long history of artificial selection in non-wild stock had left these turkeys with insufficient genetic diversity for success in the wild. In 1985, Stangel et al. (1992) initiated a survey to characterize levels of genetic diversity in eastern wild turkeys, game-farm turkeys, and domestic turkeys. Using allozyme markers, the authors found significant differences in the distribution of allele frequencies among the 3 groups. Wild turkeys exhibited levels of genetic diversity comparable to that of other native game birds, whereas domestic turkeys possessed significantly less genetic diversity than wild or game farm turkeys. Game-farm turkeys exhibited a large range in genetic variability, likely due to the wide variety of different breeding strategies used by game farmers and the many different types of farms sampled for this study (Stangel et al. 1992). The authors did not find sufficient allozyme differentiation among wild, game-farm, and domestic turkeys to permit identification of domestic introgression in wild stock. However, a project is currently underway to screen a variety of DNA-based markers to assess their utility for the differentiation of wild turkeys from domestic breeds. A higher level of variability in DNA-based markers as compared to allozyme markers increases the probability of finding ways to detect domestic introgression into wild turkey stock.

Population-level Applications

Genetic Bottlenecks/Founder Effects

Genetic bottlenecks, resulting in a loss of genetic diversity, can occur as a result of genetic drift when a population is reduced in size for many generations (Nei et al. 1975). Founder effects, a related phenomenon, refer to the change in allelic composition when a small subset of one population is used to establish a new population, leading to allele frequencies that differ from those of the original population. In both phenomena, the effect is more pronounced when the bottlenecked or founding population is small (Baker and Moeed 1987, Merila et al. 1996, Mock et al. 2004). Populations established via translocation programs are at risk for diversity losses and changes in allelic composition as a result of both processes. A number of empirical studies have demonstrated significant reductions of genetic variability in translocated wildlife populations relative to their sources (Fitzsimmons et al. 1997, Williams et al. 2000, Williams et al. 2002, 2003b). Translocated populations also may exhibit shifts in allele frequency distributions relative to their source (Fitzsimmons et al. 1997, Luikart et al. 1998, Rowe et al. 1998, Williams et al. 2000), relative to

other native populations (Baker and Moeed 1987, Perez et al. 1998, Stephen et al. 2005b), or relative to theoretical expectations (Scribner and Stuwe 1994, Fitzsimmons et al. 1997). Many, if not most, extant wild turkey populations have been established as a result of translocation, both within and beyond historical range boundaries. As a result the loss of genetic diversity in populations and shifts in allelic frequency distributions are potentially very serious issues in wild turkey management.

Leberg (1991) used allozyme markers to determine if populations of wild turkeys established as a result of translocations had higher levels of genetic differentiation among populations than turkeys that have not experienced founder events. Although the total amount of genetic differentiation he found was low, likely due to the time of sample collection (see *Social and Behavioral Dynamics* section below) and the low variability of allozymes, it nonetheless was evident that reintroduced wild turkey populations exhibited higher levels of genetic differentiation among populations (presumably due to genetic drift occurring independently among populations) than did relict populations that had not experienced severe reductions in size.

Ten years later, Mock et al. (2001) used microsatellite, control region, and AFLP data to detect reduced genetic diversity in a reintroduced population of Gould's turkeys in the Huachuca Mountains of southeastern Arizona compared to relict Gould's turkey populations in Mexico. Thus, Mock et al. (2001) recommended that although this population is stable, it may benefit from supplementation of turkeys from the more diverse relict populations.

Mock et al. (2004) assessed the genetic impact of 3 well-documented translocation events in the Merriam's subspecies, each occurring approximately 50 years ago. These translocations differed in the number of source individuals used, the number of trapping sites used to capture source individuals, and the size of the habitat into which founders were established. Microsatellite data indicated that all 3 translocations exhibited reduced genetic diversity relative to their founding populations, including 1 translocated population that is now very large and robust. Unfortunately, these results suggest that losses in genetic diversity are a common consequence of translocations, even under the best of circumstances. On the basis of their findings, Mock et al. (2004) recommended particular caution in the practice of "serial translocations", where translocated populations become the source for further translocation.

Gene Flow Among Local Populations

At a regional scale, if populations within a region exchange migrants (gene flow), the potential negative effects associated with genetic drift and low population sizes may be alleviated (Wright 1978, Allendorf 1983). Furthermore, the evolution of newly established populations is not limited by the genetic contribution of founders if gene flow among regional populations is

possible. However, if dispersal among populations is low, genetic similarities between a reintroduced population and its source may persist.

Allozyme, microsatellite, and control region data have been used to characterize interactions among reintroduced populations and between reintroduced and native populations (Leberg et al. 1994, Latch and Rhodes 2005). Leberg et al. (1994) utilized allozymes to determine whether the genetic similarities among populations were more affected by geographic proximity or by shared reintroduction histories. The authors found that reintroduced populations from common sources were more similar than expected given their geographic proximity, even decades after the reintroduction events. Therefore, it seems that although dispersal likely has occurred, it has not resulted in a detectable relationship between genetic and geographic distance, as would be expected in naturally occurring populations. These results also suggested that while founders make genetic contributions to the populations into which they are released, they may have a minimal effect on nearby populations (although the reverse is not necessarily true; see *Subspecies identification and hybridization in translocated populations* section above).

Latch and Rhodes (2005a) also used microsatellite and control region sequences to demonstrate that the genetic relationships between reintroduced populations and their sources are not quickly eroded by dispersal from nearby populations, corroborating the findings of Leberg et al. (1994). Taking advantage of well-documented reintroduction histories of turkey populations in Indiana, the authors assessed the degree to which gene flow among reintroduced populations has obscured genetic signatures left by the founding events. Effects were measured in regions characterized by high habitat continuity and a high potential for dispersal among populations and as well as in regions where the opportunity for dispersal among populations was reduced due to the low density of turkey populations. The genetic signatures left by reintroduction events were strongly evident in most populations, even after several decades. Latch and Rhodes (2005a) further showed that the density of populations in a region did not significantly affect these relationships. For each of the reintroduced populations, the authors were able to identify the magnitude of the effect of dispersers, as well as their most likely population of origin. Despite a few cases in which the apparent presence of individuals from prior reintroductions significantly impacted the genetic structure of populations, the results of this study indicated an overall paucity of gene flow among reintroduced populations in Indiana, even where the opportunity for dispersal appeared high.

Social and Behavioral Dynamics

The underlying social organization of most wild species often can be difficult to resolve (Sugg et al. 1996). The social structure, mating tactics, and movement behaviors of a species ultimately sculpt the temporal and spatial patterns of genetic structure that it

exhibits (Chesser 1991a, Chesser 1991b, Chesser et al. 1993). Therefore, examination of fine-scaled genetic structure in wild species can in turn lead to a clearer understanding of social and behavioral dynamics. In the wild turkey, interpreting patterns of genetic structure within localized regions may provide insight into the social organization of wintering flocks, interactions among flocks, and the mechanisms involved in the dissociation of flocks in the spring.

Leberg (1991) found that within regions, almost none of the allozyme variability he found in wild turkeys was accounted for by differences among sampling localities. However, the opposite result was found in Kansas, where allozymes revealed significant genetic variability among wintering flocks (Rhodes et al. 1995). Boone and Rhodes (1996) also found significant allozyme differentiation between two winter flocks in South Carolina. Latch and Rhodes (2005b) used microsatellites, control region sequences, and previously-collected allozyme data (Boone and Rhodes 1996) to investigate the reason for this dichotomy regarding genetic differentiation at a local scale. It appears that timing and method of sample collection are responsible for the discrepancy between estimates of local genetic structure. Leberg (1991) utilized samples from male turkeys collected during the spring, whereas Rhodes et al. (1995) and Boone and Rhodes (1996) used samples from both sexes of turkeys collected during winter trapping activities. In winter, samples are collected from discrete flocks, and thus genetic differentiation can be detected among them (Rhodes et al. 1995, Boone and Rhodes 1996, Latch and Rhodes 2005b). However, flocks dissociate in the spring; thus, spring-collected samples from a given geographic location contain turkeys from multiple flocks and do not exhibit local genetic structure (Leberg 1991, Latch and Rhodes 2005b). These results emphasize the need to interpret genetic data in light of the social organization of the species at the time of sample collection. These studies also have demonstrated the utility of molecular markers, both protein- and DNA-based, for investigating small scale genetic structure.

Very recently, microsatellite loci have been used to investigate kin selection and cooperative courtship in the wild turkey (Krakauer 2005). He used genetic data to estimate relatedness among individuals in a flock, and combined with data on reproductive success was able to demonstrate that the indirect fitness benefits obtained by non-breeding subordinate males offset the cost of helping. It is rare that a long-standing controversial theory such as kin selection can be confirmed, but this certainly is an example of where incredible progress can be made when the appropriate molecular tool is applied to a species in which the biology is well understood.

Individual-level Applications

Identification of individual animals has a multitude of potential applications for wildlife forensics: assignment of population or subspecies origin, studies of dis-

persal and migration, and detection of hybridization and introgression (Manel et al. 2002, Randi and Luchini 2002, Cegelski et al. 2003, Haig et al. 2004, McLoughlin et al. 2004). Cases of poaching also could benefit from individual identification, where individual animals may be classified by location of harvest.

Additionally, mark-recapture studies based on individual molecular-based identification could be a valuable non-invasive method for estimating population sizes in managed populations (Mowat et al. 2002, Wilson et al. 2003). At a local scale, individual identification and measures of relatedness among individuals can be used to characterize family groups in wildlife studies, providing insight into behaviors such as paternity and mate choice (Okada and Tamate 2000, Kerth et al. 2002, Nievergelt et al. 2002).

Microsatellite loci are currently the marker of choice for identifying individual turkeys. High levels of polymorphism in microsatellites mean that this marker type is generally associated with lower probabilities of identity (the probability that two randomly chosen individuals will have the same multilocus genotype) than other marker types. Using 10 of the microsatellite loci most commonly used in turkeys, we can achieve an overall probability of identity of 3.5×10^{-14} , almost ensuring that species-wide, no two turkeys will share a multilocus genotype (Latch 2004). This attests to the tremendous power of multilocus microsatellite genotypes in individual identification. Highly variable microsatellites have been used successfully to assign individual turkeys to a population or subspecies (Latch and Rhodes 2005, Latch et al. 2006b) and to identify migrant individuals into a recently established population (Latch et al. 2006b). Assignment tests using the available set of microsatellite loci proved to be extremely useful for detecting and characterizing hybridization between wild turkey subspecies (Latch et al. 2006a, b). Ongoing research will determine the utility of these markers for detecting introgression of domestic genes into wild stock and for providing evidence in poaching cases.

CONCLUSIONS

A suite of molecular markers has been optimized for use in the wild turkey, representing an array of marker systems (protein- and DNA-based markers), inheritance patterns (biparental and maternal), and mutation rates. The body of existing research using molecular markers in the wild turkey illustrates their power for applications ranging from the subspecies-level to the individual-level, and for questions ranging from species evolution to forensics.

Highly variable markers such as nuclear microsatellites are particularly useful for elucidating genetic structure among turkey populations, and even for identifying individual birds. Maternally-inherited mitochondrial DNA markers such as cytochrome b and control region sequences exhibit less variability among individuals, but may be indispensable in questions regarding hybridization, sex-biased dispersal, and female

lineage establishment. Low levels of genetic variability in allozymes have not precluded their use in the wild turkey; however, high levels of variability in DNA-based markers make them ideal candidates for studies of genetic variation in wild turkeys. Fortunately, several studies, including one in the wild turkey, have shown that allozyme data corroborates with data obtained from DNA-based markers (Spruell et al. 2003, Zhou et al. 2003, King and Eackles 2004, Latch 2004).

It has become apparent that the tools of modern molecular biology hold great value for wild turkey management. It also is clear that decisions pertaining to the selection of genetic markers, both in terms of inheritance patterns and rates of evolution, are important if these tools are to be applied successfully at varying scales of biological organization. In the wild turkey, appropriate utilization of molecular tools has led to a better understanding of the evolutionary history of turkeys, their behavior, and their population dynamics, which in turn can be used to manage populations to optimize growth and long-term stability. Similarly, genetic evaluations of previous translocations have advanced our understanding of founder events and post-translocation processes within and among populations.

The future of wild turkey management looks bright. The application of molecular tools will continue to advance our understanding of wild turkey biology and ecology, thereby improving our ability to effectively manage this species. Recent advances in our ability to determine the genetic composition (subspecies status) of individual animals, or even entire regions, have profound implications for the future of wild turkey management. We are now able to objectively determine what subspecies exist in what areas, and if turkeys in that area show evidence of hybridization with another subspecies. Another area of wild turkey management likely to show incredible growth is the prosecution of poaching cases. The ability of molecular tools to enable identification of individual animals and analysis methodology to assign individuals to a population of origin means that in many instances, poached animals can be objectively identified with confidence. Molecular tools may also advance our understanding of wild turkey biology, particularly at a local scale. We should be able to determine the genetic relationships among individuals within flocks, and such data could be combined with radio-telemetry data to better understand the movements and associations of turkeys within a flock throughout the year. It is an exciting time to be involved in wild turkey management, and we feel that molecular tools offer a unique perspective by which we can optimize wild turkey translocation strategies and management programs to ensure the future of this species.

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