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GENE FLOW AND GENETIC CHARACTERIZATION OF NORTHERN GOSHAWKS BREEDING IN UTAH

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Abstract. Adult movement and natal dispersal data demonstrate that Northern Goshawks (*Accipiter gentilis*) are able to travel over long distances, suggesting a large functional population. However, these data are unable to determine whether these movements contribute to gene flow among adjacent breeding areas. We used eight microsatellite DNA loci and mitochondrial DNA control-region sequence data to assess population structure of Northern Goshawks breeding in Utah. Goshawks had moderate levels of genetic variation at microsatellite loci (observed heterozygosity = 50%), similar to levels found in other medium-sized, highly mobile birds. Overall estimates of interpopulation variance in microsatellite alleles (F_{ST} = 0.011) and mtDNA haplotypes (Φ_{ST} = 0.126) were low and not significantly different from zero. Pairwise population comparisons using microsatellite markers revealed no differentiation among sampled sites, indicating that the functional population extends beyond Utah. However, pairwise population analyses of mtDNA uncovered a single case of differentiation between goshawks inhabiting Ashley National Forest, in northeastern Utah, and Dixie National Forest, in southwestern Utah. Low levels of population structuring observed in mtDNA between the two forests may be due to the smaller effective population size sampled by mtDNA, a cline of haplotypes across the West, or the presence of a contact zone between *A. g. atricapillus* and goshawks of southern Arizona and the Mexican Plateau.

Key words: Accipter gentilis, *gene flow, microsatellite loci, Northern Goshawk, population structure*

Flujo Genético y Caracterización Genética de *Accipiter gentilis* Reproduciéndose en Utah

Resumen. Datos sobre el movimiento de los adultos de *Accipter gentilis* y la dispersión natal demuestran que *A. gentilis* es capaz de viajar largas distancias, lo que sugiere una gran población funcional. Sin embargo, dichos estudios no son capaces de determinar si estos movimientos contribuyen al flujo genético entre las áreas de reproducción. En este estudio se utilizaron ocho loci de microsatélites de ADN y secuencias de la región control del ADN mitocondrial para estimar la estructura poblacional de la unidad reproductiva de *A. gentilis* en Utah. Este halcón presentó niveles intermedios de variación genética en loci de microsatélites (heterocigosidad observada = 50%), similares a los niveles encontrados en otras aves de tamaño medio con gran dispersión. La estimación total inter-poblacional de la varianza en alelos de microsatélites (F_{ST} = 0.011) y haplotipos de ADNmt (Φ_{ST} = 0.126) resultaron ser bajas y no significativamente diferentes de cero. Las comparaciones entre pares de poblaciones utilizando marcadores de microsatélites no mostraron diferencias entre los sitios muestreados, indicando que la población funcional se extiende más allá de Utah. Sin embargo, el análisis con ADNmt entre pares de poblaciones mostró en un sólo caso una diferenciación entre la población de *A. gentilis* que habita en el Bosque Nacional Ashley al noreste de Utah y la población de *A. gentilis* del Bosque Nacional Dixie, al sureste de Utah. Los niveles bajos de estructura poblacional observados con ADNmt entre los dos bosques pueden deberse a un bajo tamaño poblacional efectivo muestreado con ADNmt, a una disminución de haplotipos hacia el oeste o a la presencia de una zona de contacto entre *A. g. atricapillus* y *Accipiter gentilis* del sureste de Arizona y la meseta Mexicana.

INTRODUCTION

The Northern Goshawk is a partial migrant, with populations composed of migratory and resident individuals (Kenward et al. 1981, Widén 1985), that breeds in Holarctic temperate and boreal forests (Squires and Reynolds 1997). Over the past decade, the population viability of Northern Goshawks (*Accipiter gentilis*) breeding in southwest North America has been a concern (Kennedy 1997, Graham et al. 1999). To adequately assess the population viability of a species, it is important to define what areas constitute an in-

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terbreeding population and to determine whether populations are demographically independent. If Northern Goshawk populations are constrained to habitat patches, isolated populations may decline in genetic variability over time, affecting population viability and persistence (Frankham 1996). Dispersal data from band recoveries (1860 km, Evans and Sindelar 1974), radio-telemetry, (185 km, Squires and Ruggiero 1995; >100 km, Stephens 2001), and satellite telemetry (613 km, Sonsthagen 2002), demonstrate that breeding adults are capable of extensive movements. Nevertheless, since adults exhibit high breeding-territory fidelity (males 76%, females 71%; Detrich and Woodbridge 1994) and short breeding dispersal (males 2.8–6.5 km, females 5.2–9.8 km; Detrich and Woodbridge 1994, Reynolds and Joy 1998), these movements may not contribute to gene flow among goshawk populations. Therefore, natal dispersal may be a key component to maintaining gene flow among Northern Goshawk populations. Juvenile goshawks disperse over long distances (males 10.0–23.0 km; females 15.0–115.0 km; Detrich and Woodbridge 1994, Reynolds and Joy 1998), which may have a homogenizing effect on genetic makeup of adjacent breeding populations.

Despite concerns about Northern Goshawk population viability, no published studies to date have assessed population structure within the species. Natal dispersal data can inform hypotheses about population structure of goshawks. However, natal dispersal data are difficult to collect mainly due to difficulty recovering bands outside of the area studied. Additionally, it is difficult to assess whether movements, by breeding adults or juveniles, contribute to gene flow among populations. Therefore, we used data from biparentally inherited microsatellite loci and maternally inherited mitochondrial DNA to characterize genetic variability and assess population structure of Northern Goshawks breeding in the six National Forests in Utah. Both marker types have been useful in assessing population genetic parameters and gene flow in many species (e.g., Paetkau et al. 1997, Nesje et al. 2000, Reusch 2002, Scribner et al. 2003, Pearce et al. 2004). Since Northern Goshawks are capable of extensive movements, and females show lower site fidelity than males, we hypothesized that both mitochondrial DNA and microsatellite data collected from Northern Goshawks would reflect high levels of gene flow throughout sampled sites in Utah.

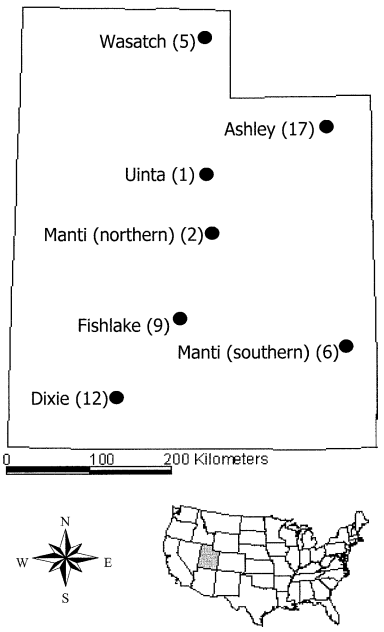

FIGURE 1. Locations of sites where Northern Goshawks were sampled for genetic analyses in the six national forests in Utah. Sites are named for the national forest on which they were located; numbers in parentheses are the number of individuals sampled.

METHODS

FIELD TECHNIQUES

Forty-six adult female and six adult male goshawks were captured at nest sites throughout the six national forests in Utah in 2000–2002: Ashley (n = 17), Dixie (n = 12), Fishlake (n = 9), Manti LaSal (n = 8), Uinta National Forest (n = 1), and Wasatch (n = 5; Fig. 1). A live Great Horned Owl (*Bubo virginianus*) was used to lure breeding goshawks at their nest sites (Rosenfield and Bielefeldt 1993) into a modified dho-gaza net trap (Clark 1981), which was set according to McCloskey and Dewey (1999). Birds were marked with U.S. Fish and Wildlife Service aluminum bands and plastic alphanumeric violet color bands. Blood was taken from the brachial vein using heparinized needles and stored in 2.0-mL storage vials in blood lysis buffer (0.1 M Tris-HCl [pH 8.0], 0.1 M EDTA, 0.1 M NaCl, and 0.5% SDS; Longmire et al. 1988).

ISOLATION OF GENOMIC DNA

Samples were kept at room temperature until DNA extraction and then stored at −80°C. Genomic DNA was extracted from each blood sample using a ''salting out'' protocol described in Medrano et al. (1990), modified by substituting 0.7 volumes of 2-propanol in place of two volumes of ethanol. Samples were treated to remove polymerase chain reaction (PCR)-inhibitory effects of heparin (Taylor 1997). Genomic DNA extractions were quantified using fluorometry and diluted to 50 ng μL^{-1} working solutions.

DEVELOPMENT OF GOSHAWK MICROSATELLITE LOCI

Primers used for microsatellite genotyping in goshawks were obtained in two ways: via cloning of goshawk microsatellite loci and via cross-species screening of microsatellite primers developed for other raptor species. Development of primers via cloning followed procedures outlined in Knowlton et al. (2003), using a goshawk sampled from the Alexander Archipelago, Alaska. This procedure yielded four primer pairs flanking microsatellite repeats, which were screened for variability using a subset of at least 24 individuals. Of these, only one locus (Age07) was found to be polymorphic in Utah goshawks. All sequence information from this microsatellite library, including novel genomic sequences not containing microsatellite core repeats and those containing repeats found to be monomorphic for individuals screened, were deposited in GenBank (accession numbers AY704665–AY704669).

We screened 24 goshawks at 29 microsatellite loci known to be variable in other raptor species including Gyrfalcon (*Falco rusticolus*), Peregrine Falcon, (*F. peregrinus*; Nesje and Røed 2000, J. Fickel, unpubl. data), Bearded Vulture (*Gypaetus barbatus*; Gautschi et al. 2000), and other accipitrids (K. Scribner, unpubl. data). An additional 10 microsatellite loci, including two sex-linked loci (*Z*-specific) known to be variable for other avian species (Fields and Scribner 1997, Buchholz et al. 1998) were also screened for variation in goshawks.

Individuals found to be homozygous at each polymorphic locus were cycle-sequenced following manufacturer's protocols (Epicentre Technologies, SequiTherm™ EXCEL II DNA Sequencing Kit-LC, Madison, Wisconsin). Sequences from the Northern Goshawk homozygotes were examined to determine that repeat motif and flanking sequence were comparable to that from the species for which they were developed. Primer sequences were redesigned as necessary, and sequence information from the loci found to differ in flanking region or repeat motif from cloned original species was deposited in GenBank (accession numbers AY704664, AY714245–AY714250).

MICROSATELLITE GENOTYPING

Forty-four individuals, those trapped during 2000 and 2001, were genotyped at each of eight microsatellite loci (Table 1). For genotyping, the forward primer for each primer pair was synthesized with an additional modified 19–20-bp tail (M13F[-29] or M13Rev; Table 1.) added to the 5′ end of the oligonucleotide (Steffens et al. 1993, Oetting et al. 1995). A primer with the sequence complementary to the specific tail, directly labeled to the infrared fluorophore IRD700 or IRD800, was used as the fluorescently labeled primer for the detection of alleles. PCR amplifications were carried out in a final volume of 10 μL and contained 2–100 ng genomic DNA, 0.2 mM dNTPs, 10 *p*mole unlabeled primers, 1 *p*mole IRD-labeled primer, 0.1 μg BSA, 1× PCR buffer (Perkin Elmer Cetus I), and 0.2 units Amplitaq DNA polymerase (PE Biosystems, Forest City, California). PCR reactions began at 94°C for 1.5 min and continued with 40 cycles each of 94°C for 30 sec; 50–56°C for 30 sec; 72°C for 1 min. For microsatellites with longer allele lengths, a 30-min extension at 72°C concluded each reaction.

The fluorescently labeled PCR products were electrophoresed on a 48-well 6% polyacrylamide gel on a LI-COR 4200LR automated sequencer (LI-COR, Lincoln, Nebraska). Initially, six individuals were scored against a fluorescently labeled M13 sequence ladder of known size. Two individuals that were heterozygous at each locus were selected among the six sized individuals and included in all subsequent genotyping gels as size standards typically occupying six lanes. For quality control purposes, 10% of the samples were extracted, amplified, and genotyped in duplicate.

MITOCHONDRIAL DNA SEQUENCING

The gene order of the mitochondrial genome of the goshawk has not been verified, but data from

TABLE 1. Primer name, tail, and primer sequence for the eight microsatellite loci used to examine genetic differentiation in Northern Goshawks across Utah. Asterisks denote previously unpublished primers, or those redesigned for the goshawk from published sequences (see text for GenBank accession numbers). For each primer pair, F denotes the forward primer and R denotes the reverse primer sequence.

Primer	Tail[a]	Primer sequence (5′-3′)	Source
Age07 (F)*	M13F (−29)[b]	AGATGGAGCCCCAAAGTC	This study
Age07 (R)*		CCAATCAACCACTACCACG	
BV11 (F)	M13F (−29)[b]	TGTTTGCAAGCTGGAGACC	Gautschi et al. 2000
BV11 (R)		AAAAGCCTTGGGGTAAGCAC	
BV13 (F)	M13Rev[c]	TTCAGGAAACAGAAGCATGAAC	Gautschi et al. 2000
BV13 (R)		AGTTTTCACATTTTCATAAG	
BV20 (F)*	M13F (−29)[b]	GCACAGCACTGAACGTGAGC	Gautschi et al. 2000
BV20 (R)		GTTTCTCCTGACAGTGAAATAACTC	
NVH142 (F)	M13Rev[c]	CCACCCCTCTGCCACTCA	Nesje and Røed 2000
NVH142 (R)		CCCCTGTCAGCTAAACACATCAC	
NVH195 (F)	M13Rev[c]	CGTACTTTAGGCTACTGAATAA	Nesje and Røed 2000
NVH195 (R)		TTAAGACAAAACGATAGACTGT	
NVH203 (F)	M13Rev[b]	CAGACCTGGCTGCAATGAGGA	Nesje and Røed 2000
NVH203 (R)		GACGACCCACGGACTACAGCTTT	
NVH206 (F)	M13Rev[b]	ATCTAATGGGCTTTCCTGGATTT	Nesje and Røed 2000
NVH206 (R)		GACATTTTCCTCATAGGCAACTGA	

[a] The forward primer of each pair was synthesized with an additional 19–20-bp tail on the 5′ end.
[b] Sequence: CACGACGTTGTAAAACGAC.
[c] Sequence: GGATAACAATTTCACACAGG.

other raptor species suggest the goshawk mtDNA genome is likely organized in the ''novel'' arrangement described in Mindell et al. (1998). Under that assumption, we developed PCR primers for goshawk mtDNA and used them to amplify the portion of the control region corresponding to domain I of the avian mitochondrial DNA (Baker and Marshall 1996). These included the light-strand primer L16064 (5′-TTG GTCTTGTAAACCAAAGA-3′) and the heavy strand primer H15426 (5′-CACCAAAGAGCAA GTTGTGC-3′). Primers were synthesized with added universal sequences (BluescriptT7P; GTA ATACGACTCACTATAGGGC; and M13Rev) on the light and heavy strand primers, respectively. PCR products were electrophoresed in TBE (89 mM Tris, 89 mM Boric Acid, 2 mM EDTA) against a 100-bp DNA ladder on a 1.5% agarose gel stained with ethidium bromide and visualized under ultraviolet light. PCR products were purified using Quantum Prep® PCR Kleen Spin Columns (BIORAD, Hercules, California). Purified products were cycle-sequenced via simultaneous bidirectional sequencing (SBS; LI-COR 1999) using a commercial kit (Sequitherm LCII 2.0®: Epicentre Technologies). We used fluorescently labeled universal primers, (LI-COR; BluescriptT7P and M13Rev) to prime the SBS reaction. We used the method described in Lanctot et al. (1999) to verify that the sequences obtained were true mtDNA sequences rather than from a nuclear pseudogene (Sorenson and Fleischer 1996). For quality control purposes, DNA from two to five individuals representing each designated subpopulation were extracted, amplified, and sequenced in duplicate. MtDNA sequences were electrophoresed on a 64-well 3.7% polyacrylamide gel on a LI-COR 4200LR automated sequencer, analyzed using LI-COR eSeq™ imaging software and aligned using AlignIR 2.0™.

STATISTICAL ANALYSIS

Goshawks trapped in Utah were grouped into proposed populations by national forest or geographic proximity. Individuals trapped on the Uinta and Wasatch National Forests (northern Utah) were treated as one population based on proximity of nest sites, forest corridor connecting these sites, and limited sample size from both forests. Allelic frequencies and observed and expected heterozygosities were calculated in GENEPOP version 3.1 (Raymond and Rousset 1995) to summarize variation at microsatellite loci. Each locus in the proposed populations was tested for deviation from Hardy-Weinberg equilibrium in GENEPOP, using the Markov chain parameters provided (dememorization number = 1000, number of batches = 100, and number of iterations per batch = 1000). Since loci were not mapped, each pair of loci was tested for linkage disequilibrium in GENEPOP using the Markov chain parameters provided. We used ARLEQUIN 2.0 (Schneider et al. 2000) to estimate haplotype (h) and nucleotide (π) diversity (Nei 1987, Eq. 8.4 and 10.6, respectively).

F-statistics (F_{IT}, F_{ST}, and F_{IS}) were used to estimate subdivision among the sampled populations and were obtained using FSTAT Version 2.9.3 (Goudet 1995, 2001). F_{IT} is a measure of deviation from Hardy-Weinberg equilibrium, F_{ST} is a measure of the genetic differentiation among populations where values range from 0 (panmixia) to 1 (no gene flow), and F_{IS} is a measure of deviations from Hardy-Weinberg equilibrium within populations. The method of Weir and Cockerham (1984) was used to correct for small sample size. Confidence intervals were used to determine whether F_{ST} was significantly greater than zero. Pairwise F_{ST} comparisons of populations were calculated in ARLEQUIN 2.0. Global R-statistics were calculated in FSTAT (Slatkin 1995) and pairwise R-statistics were calculated in ARLEQUIN 2.0. Significance of heterogeneity of mtDNA haplotypes between populations was tested using the MONTE function in the program REAP (Ver 4.0, McElroy et al. 1991) and using 5000 replicates based on the Monte Carlo χ^2 test of Roff and Bentzen (1989). Global Φ_{ST} for sequence data was calculated in FSTAT. We used the maximum-likelihood criterion in Modeltest 3.06 (Posada and Crandall 1998) to determine the evolutionary model that best fit the sequence data. These distances were used to calculate pairwise Φ_{ST} (Excoffier et al. 1992) and tested for significance using ARLEQUIN 2.0. We tested the hypothesis of selective neutrality for mtDNA control region sequence data, and for historical fluctuations in population demography, using Fu's Fs (Fu 1997) and Tajima's D (Tajima 1989) implemented by ARLEQUIN. We applied critical significance values of 5%. This significance value requires a P-value below 0.02 for Fu's Fs (Fu 1997). Significantly large negative Fs values can be interpreted as evidence of population expansion.

TABLE 2. Pairwise F_{ST} values and R_{ST} values calculated from microsatellite data and Φ_{ST} values calculated from mtDNA sequence data for each pair of five Northern Goshawk populations in Utah (calculated in ARLEQUIN, Schneider et al. 2000). Significant pairwise comparisons are denoted with an asterisk. Individuals breeding in Uinta and Wasatch National Forests were treated as one population; individuals in northern and southern Manti National Forest were treated as a separate single population.

Populations	F_{ST}	R_{ST}	Φ_{ST}
Ashley vs. Dixie	−0.005	0.004	0.126*
Ashley vs. Fishlake	0.025	0.003	0.063
Ashley vs. Manti	−0.013	−0.034	0.030
Ashley vs. Wasatch/Uinta	0.012	0.016	–0.101
Dixie vs. Fishlake	0.014	−0.016	0.016
Dixie vs. Manti	–0.009	0.015	0.072
Dixie vs. Wasatch/Uinta	0.017	0.033	0.002
Fishlake vs. Manti	–0.011	–0.012	–0.001
Fishlake vs. Wasatch/Uinta	0.004	–0.025	–0.138
Manti vs. Wasatch/Uinta	0.025	0.052	−0.032

MIGRATE version 1.8.2 (Beerli 1998, 2002, Beerli and Felsenstein 1999), available through the LAMARC package, calculated actual estimates of number of migrants per generation (N_em) for microsatellite data and number of female migrants per generation (N_fm) for mtDNA data. Isolation by distance was calculated among populations in IBD (Bohonak 2002) using default parameters provided to assess if more geographically distant population pairs were also more genetically different. Slatkin's (1993) similarity measure, *M*, was obtained using F_{ST} values calculated in FSTAT and ARLEQUIN. Microsatellite data were analyzed in STRUCTURE (Pritchard et al. 2000) to detect the occurrence of population structure without *a priori* knowledge of putative populations. This program uses multilocus allelic frequencies to assign individuals probabilistically to populations. Data were analyzed using an admixture model assuming correlated frequencies among populations, and results are generated from 10 000 Markov chain Monte Carlo iterations following a burn-in period of 10 000 iterations with number of possible populations (*K*) ranging from 1–10. This analysis was repeated 30 times for each value of *K* to ensure that results were consistent across runs, as suggested by Pritchard et al. (2000). Data were analyzed in MIGRATE using populations determined by STRUCTURE.

RESULTS

MICROSATELLITE DATA

Complete multilocus genotypes were obtained for 44 individuals across eight polymorphic loci. The number of alleles per locus ranged from 2–11 and observed heterozygosity for each population ranging from 46% to 59% with an overall value of 50% (Sonsthagen 2002). There were no significant deviations from Hardy-Weinberg equilibrium for any loci within or across populations ($F_{IS} = -0.084 \pm 0.061$, $F_{IT} = -0.072 \pm 0.034$). We observed no linkage disequilibrium among loci (Sonsthagen 2002). The overall F_{ST} (0.011 ± 0.025) was not significantly greater than zero, indicating lack of population subdivision. No population pairwise F_{ST} values were significantly different from zero (Table 2). Similarly, overall ($R_{ST} = -0.004$) and pairwise R_{ST} values were not significantly greater than zero (Table 2), supporting the F_{ST} results.

The number of populations for the most likely model generated by STRUCTURE varied across runs, suggesting sample size was too low or from too small of a geographic area to use this approach. Since we were unable to assign individuals to populations using STRUCTURE, we tested a two-population model in MIGRATE by combining the national forests into groups based on satellite telemetry data (Sonsthagen 2002). One population was composed of national forests from northern Utah (Ashley, northern Manti, Uinta, and Wasatch National Forests) and another from national forests from the southern region (Dixie, Fishlake, and southern Manti National Forests). N_em calculated in MIGRATE under this two-population model were greater than one migrant per generation for each population, with asymmetrical rates ($N_em = 20.2$ from the northern population into the southern population and $N_em = 14.9$ from the southern population into the northern population), sug-

TABLE 3. Number, nucleotide (π) and haplotype (h) diversity, and sequence differences of eight mtDNA control-region haplotypes in 49 Northern Goshawks in Utah. Position numbers (read vertically) refer to the location of each variable site in the sequence. Dots indicate similarity with haplotype A. Individuals breeding in Uinta and Wasatch National Forests were treated as one population; individuals in northern and southern Manti National Forest were treated as a separate single population.

	Number of haplotypes per location					Position
Haplotype	Ashley	Dixie	Fishlake	Manti	Wasatch/ Uinta	2 2 3 3 3 3 3 3 4 7 1 2 2 3 7 5 7 0 4 8 8 1
A	3	1	1	2	1	T G C G C T A
B	11	2	5	3	3	. . . A . . .
C	1	0	0	0	0	C . . . . . .
D	1	3	1	0	1	. A . A . . .
E	1	0	1	0	0	. . . A . C .
F	0	4	1	0	0	. . . . . . G
G	0	1	0	1	0	. . T A . . .
H	0	0	0	1	0	. . T A T . .
Total	17	11	9	7	5	
h	0.574	0.818	0.722	0.809	0.700	
π	0.002	0.008	0.004	0.005	0.002	
Fu's *Fs*	−2.141*	−0.813*	−2.360*	−1.059*	−0.829*	
Tajima's *D*	−1.158*	−0.223	−1.149*	−0.050	−0.972*	

* Significant *P*-values for Fu's *Fs* ($P < 0.02$) and Tajima's *D* ($P < 0.05$).

gesting panmixia. IBD analysis uncovered no significant correlations between genetic and geographical distances.

MTDNA SEQUENCE DATA

Nucleotide sequence data comprising 562 bp from the mtDNA control region were collected from 49 goshawks in Utah. Sequences are accessioned in GenBank (accession numbers—AY699828–AY699835). There were eight unique haplotypes across all forests (Table 3). Analysis of mtDNA sequence data, using Modeltest 3.06 (Posada and Crandall 1998) suggested the best evolutionary model fit to the data was the $HKY_{(\Gamma = 0.005)}$ model (Kimura 1980) under the hierarchical likelihood-ratio criterion. We detected no significant differences among subpopulations in the distribution of haplotypes using Monte Carlo χ^2 simulation ($P = 0.16 \pm 0.03$), or variance in haplotype frequency ($\Phi_{ST} = 0.033$; $P = 0.27 \pm 0.01$, $\chi^2 = 31.8$) overall. Significant pairwise population differentiation was observed only between the Ashley and Dixie National Forests (Table 2). Haplotype (h) and nucleotide (π) diversity ranged from 0.574 to 0.818 and 0.002 to 0.008 respectively (Table 3). Significant negative values calculated for Fu's *Fs* and Tajima's *D* indicated population expansion. Using the population combinations as with the microsatellite data, we tested a two-population model in MIGRATE using mtDNA sequences. As with the microsatellite data, N_fm calculated in MIGRATE were greater than one migrant per generation for each population ($N_fm = 1.6$ from the northern population into the southern population and $N_fm = 1.2$ from the southern population into the northern population), suggesting panmixia.

DISCUSSION

Levels of genetic variation for Northern Goshawks breeding in Utah appear to be moderate relative to other avian species. Other studies of similar sized, highly mobile birds have demonstrated observed heterozygosities of 32% (Gyrfalcon; Nesje and Røed 2000), 45% (Peregrine Falcon; Nesje et al. 2000), 7–90% across 14 loci (Bearded Vulture; Gautschi et al. 2000), and 68% (Common Raven [*Corvus corax*] and American Crow [*C. brachyrhynchos*]; Tarr and Fleischer 1999).

We were unable to detect significant population subdivision among sampled sites using biparentally inherited markers, which is consistent with the broad, shallow clines, and lack of morphometric population structuring throughout the western interior U.S. shown by Whaley and White (1994). Our estimate of gene flow was much higher than required to maintain panmixia ($N_em = 1$; Slatkin 1987). We are aware of the

issues regarding estimates of gene flow using F_{ST}-based estimators (Bossart and Prowell 1998) and do not suggest the N_em values reported here are absolute. Rather, we present them heuristically to illustrate relative differences in estimates of past rates of gene flow (integrated over several generations) among the populations analyzed. Nevertheless, our analyses suggested that the functional population of Northern Goshawks breeding in Utah extends beyond the sampled area. Given that adults have high breeding-territory fidelity and short dispersal distances (Detrich and Woodbridge 1994, Reynolds and Joy 1998), we infer that gene flow is being maintained largely by natal dispersal.

Global comparisons of population subdivision calculated with mtDNA data also suggested panmixia. However, we did observe significant variance in haplotype frequencies between the Ashley National Forest in northeast Utah and Dixie National Forest in southwest Utah, indicating low levels of broad-scale population structure occurring at this marker. This pattern of genetic variation, lack of structuring at nuclear microsatellite loci but some structuring in the mtDNA, is usually attributed to the smaller effective population size of mtDNA in addition to female natal site fidelity (Avise 1994, Moritz 1994). It is possible that gene flow between populations inhabiting the Ashley and Dixie National Forests is maintained largely by males, with female philopatry sufficiently high to constrain haplotypic diversity. However, given the breeding and natal dispersal distances reported for this bird, this is unlikely since female goshawks disperse farther than males. Differences in the haplotype distribution between northern and southern national forests in Utah may also be caused by clinal variation in haplotype frequencies across the West. However, samples from a larger geographic area are needed to confirm this hypothesis. It is also possible that this subdivision reflects a contact zone occurring at the Dixie National Forest between *A. g. atricapillus* and goshawks of southern Arizona and the Mexican Plateau. Some researchers (Phillips et al. 1964, Wattel 1973, Whaley and White 1994, Squires and Reynolds 1997) place the latter goshawks into *A. g. apache*, although this subspecies was subsumed under *A. g. atricapillus* (AOU 1957, Palmer 1988). Unique haplotypes present in the southern Utah national forests may be common in *A. g. apache*.

Lack of genetic population structuring observed in this study is likely due, at least partially, to behavioral response to environmental factors, such as climate and habitat instability (McPeek and Holt 1992, Paradis 1998, Winkler et al. 2000). Birds residing in tropical regions have higher levels of population differentiation relative to temperate species, suggesting that the high environmental variability observed in temperate regions has homogenized avian genetics via increased dispersal and migratory behavior (Winkler et al. 2000). Newton (2003) suggests that raptors occupying spatially and temporally unstable environments demonstrate lower fidelity to breeding territories than those occupying more stable environments. Young birds are more vulnerable to weather extremes (Newton 1998); data on goshawk movement indicate that individuals move long distances to avoid inclement local weather conditions (Squires and Ruggiero 1995). In addition, juvenile goshawks disperse farther when local food source availability decreases (Byholm 2003, Kennedy and Ward 2003). Additionally, data collected from resident populations in south-coastal Alaska and British Columbia are genetically differentiated from adjacent migratory populations (S. Talbot, unpubl. data). A similar pattern has also been observed in House Wrens (*Troglodytes aedon* and *T. musculus*), where increased gene flow is found in migratory populations compared to residents (Arguedas and Parker 2000). Therefore, the regional and annual variability in migratory behavior exhibited by Northern Goshawks breeding in Utah likely contributes to high levels of gene flow among adjacent populations.

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