

LOW LEVELS OF GENETIC VARIABILITY IN NORTH AMERICAN POPULATIONS OF THE WOOD STORK (*MYCTERIA AMERICANA*)

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ABSTRACT.—The breeding population of Wood Storks (*Mycteria americana*) in the southeastern United States has declined since the 1930s, resulting in the listing of all United States populations of the species as endangered in 1984. We assessed genetic structure within and among nine colonies of Wood Storks from Georgia and Florida. Levels of band sharing based on multilocus oligonucleotide DNA fingerprinting of individuals from seven colonies ranged from 58% among nests within the same tree to approximately 55% within the same colony. Levels of band sharing were similar to those reported for other populations of birds that have experienced drastic reductions in population size. A more thorough analysis of four polymorphic microsatellite loci for 136 individuals from nine colonies indicated low levels of allelic diversity and low genetic divergence among colonies. Genetic differentiation ($F_{ST} = 0.015$) was similar to levels detected from allozymes for 15 colonies of Wood Storks in Florida ($F_{ST} = 0.019$). These data, together with demographic studies of these populations, indicated high levels of gene flow among colonies ($N_m = 16.4$). In agreement with previous studies, we recommend that all colonies of Wood Storks in the southeastern United States be managed on a regional basis as a single interbreeding population. Similar genetic surveys of the disjunct breeding populations of Wood Storks in South America and Central America would be beneficial in understanding the total genetic differentiation in the species. Received 3 August 1998, accepted 22 March 1999.

THE WOOD STORK (*Mycteria americana*) is a colonial-nesting wading bird of the tropical and lower subtropical zones of the Americas. The breeding range of Wood Storks is nearly contiguous where suitable habitat exists from northern Mexico to western Ecuador, eastern Peru, Bolivia, Brazil, and northern Argentina. Breeding populations of Wood Storks also are found in the southeastern United States, Cuba, and Hispaniola (AOU 1998). Although Wood Storks historically have nested in all coastal states from Texas to South Carolina, no evidence exists that colonies ever formed on a regular basis or contained large numbers of individuals in the United States outside of Florida (Ogden and Patty 1981, Ogden et al. 1987). From 1900 to 1968, the largest colonies were located in southern Florida and contained 10,000

to 20,000 individuals (USFWS 1996). Beginning in the 1930s, however, Wood Storks throughout the southeastern United States declined from an estimated 60,000 individuals to a low of 5,000 individuals in 1978 (Ogden and Patty 1981, Ogden et al. 1987). Since 1983, surveys of all known Wood Stork colonies in the southeastern United States, which occur only in Florida, Georgia, and South Carolina, produced estimates of 11,000 to 13,000 individuals (USFWS 1996). This decline has been attributed to loss or degradation of wetland habitat, water-level manipulations, predation, lack of nest tree regeneration, human disturbance, and chemical pollution (USFWS 1996). Pursuant to the Endangered Species Act, the United States Fish and Wildlife Service listed all United States breeding populations of Wood Storks as endangered in 1984.

Wood Stork breeding colonies are convenient

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management units for conservation because of their discrete geographic delineation. However, because the location of many colonies may shift because of seasonal and hydrologic changes (Ogden and Patty 1981, Kushlan and Frohring 1986, Harris 1994), breeding colonies may not be the most appropriate management units. Stangel et al. (1990) hypothesized that, following colony abandonment, adult storks disperse widely to reneest in other colonies in more favorable habitats. Thus, using colonies as management units is complicated by the unknown degree of overlap and population interchange among colonies. Although Wood Storks apparently are monogamous during each nesting season, they probably form new pair bonds every season (Kahl 1972). It is unclear how these pair bonds form because some colonies shift locations. If the colony remains intact during such shifts, and new pair bonds are formed between individuals within the colony, or if one sex is philopatric to the colony, then genetic structure should be detectable with either biparentally or uniparentally inherited loci. However, little genetic structure would be expected if the cohesiveness of the colony breaks down during colony shifts, or if annual pair bonds are formed with individuals from different colonies.

Large-scale colony shifts in concert with insufficient time for numbers of Wood Storks to increase significantly since the population decline of the 1930s have been invoked to explain the lack of significant genetic divergence among Wood Stork colonies in Florida (Stangel et al. 1990). Under these conditions, depending upon levels of genetic uniqueness and gene flow among colonies, conservation would be more effectively applied at higher levels of population structure. Once genetic structure within and between colonies is understood, it should be possible to delineate genetically appropriate management units (Moritz 1994) and to identify changes in population structure and dynamics (Prior et al. 1997).

The primary objective of our study was to assess levels of genetic variability and structure among nine Wood Stork colonies from Georgia and Florida at a higher resolution than provided by a previous allozyme study (Stangel et al. 1990). We chose to use microsatellites because they are abundant in the nuclear genome of most taxa (Baker 1994) and they evolve rapidly.

In addition to providing baseline data on levels of genetic variability within and among Wood Stork colonies, we addressed Task 3.2 of the Wood Stork recovery plan (USFWS 1996) by providing the necessary data to determine (1) whether coastal colonies should be managed differently than inland colonies, (2) the important source colonies for new colonies, and (3) the important colonies for protection and acquisition.

METHODS

Blood sampling.—We sampled blood from 136 Wood Stork nestlings (three to six weeks old) that occupied nests 2 to 25 m off the ground in nine colonies in Florida and Georgia: Dee Dot, Duval County, Florida; Grant Farm, Brevard County, Florida; Pelican Island, Indian River County, Florida; Birdsville, Jenkins County, Georgia; Blackwater, Brooks County, Georgia; Heard's Pond, Thomas County, Georgia; Brailey's Swamp and St. Simon's Island, Glynn County, Georgia; and Dover Bluff, Camden County, Georgia (Fig. 1). Blood samples (ca. 0.3 mL) were collected from the brachial vein and stored in polypropylene tubes containing 5 mL of lysis buffer; DNA was extracted from whole blood following Longmire et al. (1997).

Multilocus analysis.—Sixty-seven of the 136 individuals sampled from seven of the colonies were oligonucleotide fingerprinted (Rassmann et al. 1996) at least twice on gels containing only individuals from a single colony. Approximately 10 μ g of genomic DNA were digested to completion with an excess of the restriction endonuclease *Hinf*I under buffer conditions recommended by the supplier (Promega). After arresting the enzymatic reaction, a 1-kb ladder was added to each sample to serve as an internal size standard. Resulting fragments, along with their internal size standard, were electrophoresed in 0.8% agarose gels (20 \times 25 cm) at 30 to 35 mAmps for approximately 40 h, acid depurinated, alkali denatured, and transferred to a nylon hybridization membrane (Hybond-N+, Amersham) in 20X SSC. After baking for 2 h at 80°C, membranes were rehydrated, probed by the ECL nonradioactive detection method (Amersham) with the simple-sequence repeat motif probe (GT)_n (Pharmacia), and visualized via autoradiography.

DNA fragments from 3.1 to 12 kb were scored for all individuals. Because fragment-mobility curves varied among gels, no comparisons were made between gels. The following statistics were computed for all intracolony comparisons: mean number of bands scored, heterozygosity (Stephens et al. 1992), number of loci, number of alleles per locus, and coefficient of band sharing or similarity (Lynch 1990) using program GELSTATS (Pelikan and Rogstad

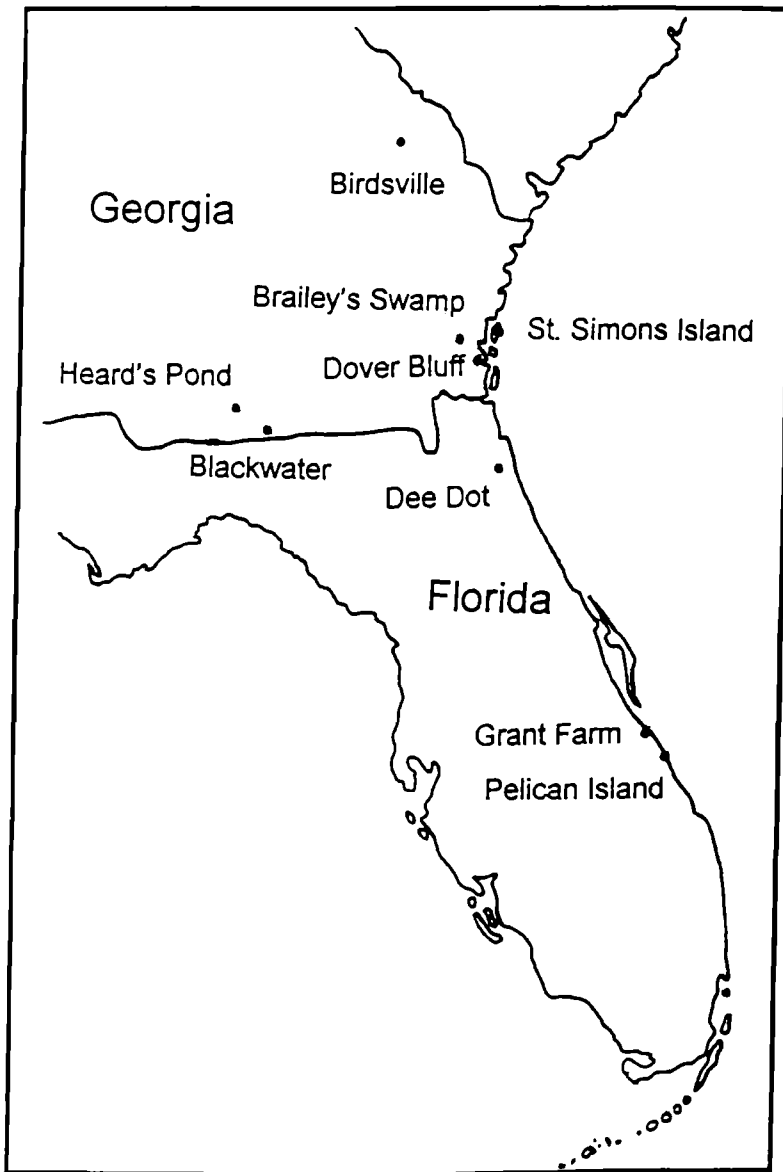


FIG. 1. Locations in Florida and Georgia of Wood Stork colonies sampled for genetic analysis of intra- and intercolony variability and differentiation.

1996). We examined various parameters of genetic variation using the following hierarchical design: nests within the same tree (11 pairwise comparisons), trees within the same colony (67 pairwise comparisons), and mean similarity values within colonies. The latter comparison was made because insufficient information for some colonies precluded comparisons of nests within trees or trees within colonies.

To compare levels of heterozygosity and similarity

between coastal and intercoastal colonies versus inland colonies, individuals from the following pairs of colonies were run on the same gel for multilocus oligonucleotide fingerprint analyses: St. Simons ($n = 9$) and Birdsville ($n = 5$) in Georgia; St. Simons ($n = 7$) and Heard's Pond ($n = 4$) in Georgia; and Grant Farm ($n = 9$) and Dee Dot ($n = 9$) in Florida. Tests for significant differences in heterozygosity and band sharing among pairwise colony comparisons were computed using the permutation tests in GEL-

STATS, which calculates a value within each population and then performs a permutation of individuals across colonies by randomly reassigning individuals to colonies and testing for significant difference in the original data and the reorganized data. The methods for conducting these permutation tests (and the advantages and disadvantages of such tests) are discussed by Pelikan and Rogstad (1996).

Single-locus analysis.—A genomic library of small insert size (200 to 400 bp) was constructed from one Wood Stork (TK 16819) using standard protocols (Weber and May 1989). Fragments containing microsatellite loci were identified by probing the library for $(GT)_n$ simple-sequence repeats, and the fragments were isolated and sequenced. Primers were designed from sequences flanking microsatellite repeats with a minimum of 12 repeats of the core motif. Ten microsatellite loci were identified and sequenced from this initial library screening. Four of these 10 microsatellite loci were used to examine genetic variation within and among Wood Stork colonies (Table 1) following standard protocols.

Standard population genetic parameters and deviations from Hardy-Weinberg proportions were tested with BIOSYS-1 (Swofford and Selander 1989) with the alpha level adjusted for multiple tests (analysis of individual loci across all populations) to give a Type I error < 0.05 (Rice 1989). The probability of identity for each locus and for each colony was calculated following Paetkau et al. (1998). Values were compared with the individual loci, and the combined probability of identity was based on assuming that all 136 of the individuals sampled represented a single randomly breeding population. The extent to which genetic variation was partitioned within and among colonies was analyzed with analysis of molecular variance (AMOVA) using the Arlequin option (Schneider et al. 1997). Significance of F_{IS} , F_{IT} , and F_{ST} was obtained using a randomization procedure with 1,000 permutations (Excoffier et al. 1992).

RESULTS

Multilocus analysis.—The number of individuals that were oligonucleotide fingerprinted, the mean number of fragments detected, the estimated number of loci examined, the mean number of alleles, average heterozygosity, and band sharing for each of the seven Wood Stork colonies are presented in Table 2. Nestlings collected from different nests within the same tree shared approximately 58% of their bands, and nestlings from different trees within the same colony shared approximately 55% of their bands. Permutation tests for intracolony and intercolony comparisons among coastal and intercoastal colonies versus inland colonies de-

TABLE 1. Locus names, microsatellite repeat, PCR primers, and annealing temperatures used to amplify four polymorphic microsatellite loci in Wood Storks.

Name	Repeat	Forward primer	Reverse primer	Temp. (°C)
WS1	$(GT)_{15}$	5'-GATCCCTTAAGGAAGCCATTTC-3'	5'-ATTGTTAATACACAGTATACCAAG-3'	47
WS2	$(A)_3G(A)_{21}$	5'-GGATCAGTGACACTGCTGCTGCTA-3'	5'-GATTTACAGTCTGGTTCAATGT-3'	64
WS4	$(GT)_{15}$	5'-TCATGTGTACACATAGGAAAAGT-3'	5'-CAGCTGAGATTTAATGGCTTTGG-3'	60
WS6	$(GT)_{14}$	5'-AGTACATGAGGAGATGGAAGTCTG-3'	5'-AGTATATACTTTCCTTCACTAGTTG-3'	54

TABLE 2. Descriptive statistics^a for genetic variation within seven colonies of Wood Storks based on oligonucleotide DNA fingerprinting analysis with the simple-sequence repeat motif (GT)_n.

Colony	<i>n</i>	No. of bands	<i>L_{bc}</i>	<i>A</i>	<i>p</i>	<i>H_{bc}</i>	<i>S</i>
Pelican Island, Florida	10	17.6 ± 4.25	13.15	3.19	0.4678	0.3611	0.6511
Grant Farm, Florida	11	28.1 ± 2.26	19.00	3.63	0.7369	0.5446	0.5167
Dee Dot, Florida	17	30.7 ± 2.11	20.28	3.80	0.8521	0.5671	0.5913
Heard's Pond, Georgia	4	19.0 ± 0.82	12.96	2.79	0.7679	0.6591	0.6125
Birdsville, Georgia	9	23.1 ± 3.52	15.30	3.73	0.8039	0.6031	0.5374
Dover Bluff, Georgia	3	20.7 ± 2.52	14.80	2.50	0.5945	0.5720	0.5019
St. Simons, Georgia	9	24.1 ± 3.66	15.40	4.14	0.8702	0.6676	0.4824

^a *n* = mean sample size per colony; No. of bands = mean (± SE) number of bands scored per individual; *L_{bc}* = bias-corrected estimate of number of loci examined (Raymond and Rousset 1995); *A* = mean number of alleles per locus; *p* = proportion of loci polymorphic; *H_{bc}* = bias-corrected estimate of heterozygosity; *S* = mean similarity (band sharing) within colonies (Lynch 1990).

tected no significant differences (*P* > 0.05) in levels of heterozygosity or similarity for any of the following pairwise comparisons: St. Simons versus Birdsville, Georgia; St. Simons versus Heard's Pond, Georgia; and Grant Farm versus Dee Dot, Florida.

Single-locus analysis.—Because microsatellite alleles are identified based on size differences only, homoplasy (i.e. comigration of alleles of the same size generated from different mutational events) is a potential problem with these types of data. Furthermore, because locus WS-2 consists of a monomeric string of adenine, homoplasy is of greater potential with this locus. Therefore, for all population genetic analyses,

alleles were designated by unique symbols, and no reference was made to actual allele size. Analyses of four microsatellite loci revealed low levels of allelic diversity among the 136 Wood Storks genotyped (Table 3). Allele frequencies did not differ significantly ($\chi^2 = 43.9$, *P* = 0.31) among colonies (Table 4). Overall probability of identity for the four microsatellite loci for individuals drawn at random from the same colony ranged from 0.041 to 0.104, compared with a probability of identity of 0.048 when all individuals were considered to be one randomly breeding population (Table 5). The mean fixation indices (*F_{IS}* and *F_{IT}*) for all loci and colonies documented a deficiency of

TABLE 3. Genotype frequency data for four polymorphic microsatellite loci detected within Wood Stork breeding colonies at Pelican Island, Florida (PIFL); Grant Farm, Florida (GFFL); Dee Dot, Florida (DDFL); Heard's Pond, Georgia (HPGA); Blackwater, Georgia (BWGA); Birdsville, Georgia (BVGA); Brailey's Swamp, Georgia (BSGA); Dover Bluff, Georgia (DBGA); and St. Simon's Island, Georgia (SSGA).

	PIFL (<i>n</i> = 18)	GFFL (<i>n</i> = 16)	DDFL (<i>n</i> = 20)	HPGA (<i>n</i> = 10)	BWGA (<i>n</i> = 10)	BVGA (<i>n</i> = 16)	BSGA (<i>n</i> = 11)	DBGA (<i>n</i> = 16)	SSGA (<i>n</i> = 19)
WS1									
176/174	0.39	0.50	0.65	0.10	0.50	0.50	0.27	0.50	0.53
176/170	0.00	0.06	0.10	0.00	0.00	0.06	0.00	0.06	0.11
174/174	0.44	0.38	0.25	0.80	0.40	0.44	0.73	0.44	0.36
174/170	0.17	0.06	0.00	0.10	0.10	0.00	0.00	0.00	0.00
WS2									
139/139	0.89	0.87	0.95	1.00	1.00	0.87	0.90	1.00	0.84
139/129	0.11	0.13	0.05	0.00	0.00	0.13	0.00	0.00	0.16
129/129	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00
WS4									
196/196	0.00	0.19	0.10	0.10	0.40	0.13	0.20	0.06	0.26
196/186	1.00	0.81	0.80	0.50	0.10	0.25	0.60	0.38	0.42
186/186	0.00	0.00	0.10	0.40	0.50	0.62	0.20	0.56	0.32
WS6									
220/220	0.17	0.25	0.15	0.00	0.00	0.25	0.27	0.13	0.05
220/210	0.61	0.19	0.30	0.80	0.60	0.13	0.46	0.31	0.42
210/210	0.22	0.56	0.55	0.20	0.40	0.62	0.27	0.56	0.53

TABLE 4. Descriptive statistics^a for genetic variation at four microsatellite loci in Wood Storks from nine colonies in Florida and Georgia.

Colony	<i>n</i>	<i>A</i>	<i>p</i>	<i>H_o</i>	<i>H_e</i>
Pelican Island, Florida	18	2.3 ± 0.3	100	0.569 ± 0.182	0.395 ± 0.097
Grant Farm, Florida	16	2.3 ± 0.3	100	0.438 ± 0.167	0.390 ± 0.900
Dee Dot, Florida	20	2.3 ± 0.3	100	0.475 ± 0.181	0.383 ± 0.114
Heard's Pond, Georgia	10	2.0 ± 0.4	75	0.375 ± 0.175	0.295 ± 0.121
Blackwater, Georgia	10	2.0 ± 0.4	75	0.325 ± 0.160	0.358 ± 0.120
Birdsville, Georgia	16	2.3 ± 0.3	100	0.281 ± 0.104	0.338 ± 0.075
Brailey's Swamp, Georgia	11	2.0 ± 0.0	100	0.332 ± 0.129	0.372 ± 0.089
Dover Bluff, Georgia	16	2.0 ± 0.4	75	0.313 ± 0.117	0.317 ± 0.107
St. Simons, Georgia	19	2.3 ± 0.3	100	0.395 ± 0.109	0.381 ± 0.097

^a *n* = mean sample size per locus; *A* = mean (± SE) number of alleles per locus; *p* = proportion of loci polymorphic at 0.95 level; *H_o* = observed heterozygosity (± SE); *H_e* = unbiased expected heterozygosity (± SE) after Nei (1978).

homozygotes ($F_{IS} = -0.120$; $F_{IT} = -0.099$), and the mean overall genetic differentiation among colonies (F_{ST}) was 0.019. These results indicated that about 98% of the total genetic variability of Florida and Georgia Wood Storks was contained within any single colony, whereas less than 2% resulted from divergence in allele frequencies among colonies. Permutation tests of mean F_{IS} , F_{IT} , and F_{ST} values indicated that none of the fixation indices differed significantly from zero.

DISCUSSION

Intracolony genetic variation.—Based on a combination of single-locus and multilocus approaches, Wood Storks in the southeastern

United States can be characterized by low levels of genetic variability and allelic diversity. Levels of band sharing within Wood Stork colonies (58% for individuals within the same tree and 55% among individuals within the same colony) are similar to observed levels of band sharing for first-order relatives in other species of birds that have not experienced population declines (Brock and White 1992, Haig and Balou 1995). Although Wood Stork numbers dropped to about 10,000 individuals in 1978 (Ogden and Patty 1981, Ogden et al. 1987), the observed levels of heterozygosity within colonies were similar to or greater than those observed in vertebrates that experienced population reductions even more drastic than those of Wood Storks (Taylor et al. 1994, Forbes et al.

TABLE 5. Probability of identity for each of the four polymorphic microsatellite loci individually, mean value of the four loci within each colony, and values for each locus for all 136 Wood Storks examined at Pelican Island, Florida (PIFL); Grant Farm, Florida (GFFL); Dee Dot, Florida (DDFL); Heard's Pond, Georgia (HPGA); Blackwater, Georgia (BWGA); Birdsville, Georgia (BVGA); Brailey's Swamp, Georgia (BSGA); Dover Bluff, Georgia (DBGA); and St. Simon's Island, Georgia (SSGA). Overall within-colony probability of identity value is the product of individual values and assumes linkage equilibrium between loci. Probability of identity value for the entire sample of Wood Storks assumes random mating of all individuals.

PIFL (<i>n</i> = 18)	GFFL (<i>n</i> = 16)	DDFL (<i>n</i> = 20)	HPGA (<i>n</i> = 10)	BWGA (<i>n</i> = 10)	BVGA (<i>n</i> = 16)	BSGA (<i>n</i> = 11)	DBGA (<i>n</i> = 16)	SSGA (<i>n</i> = 19)	Overall (<i>n</i> = 136)
WS1									
0.365	0.340	0.320	0.672	0.372	0.384	0.615	0.384	0.329	0.370
WS2									
0.808	0.779	0.906	1.000	1.000	0.779	0.687	1.000	0.738	0.853
WS4									
0.375	0.385	0.375	0.401	0.376	0.457	0.375	0.461	0.376	0.380
WS6									
0.376	0.402	0.425	0.386	0.425	0.416	0.375	0.434	0.453	0.402
Overall									
0.042	0.041	0.046	0.104	0.059	0.057	0.059	0.077	0.041	0.048

1995, Menotti-Raymond and O'Brien 1995, Houlden et al. 1996).

Should inland colonies be managed differently than coastal colonies?—Comparisons of heterozygosity and band sharing for representatives of coastal versus inland colonies detected no significant differences. These pairwise comparisons, in conjunction with examination of the probability of identity for each population (Table 5) and the results depicted in Table 2, suggest a lack of significant differences between coastal and inland populations. Although these results provide insight into the lack of genetic structure in the population, the more traditional approach for testing for population structure is through F -statistics.

Values for F_{IS} and F_{IT} are in agreement with a previous allozyme study of Wood Storks (Stangel et al. 1990). The low level of genetic divergence among Wood Stork colonies ($F_{ST} = 0.015$) indicates that only 1.5% of the total genetic variability detected in this study can be attributed to differences among colonies. This level of genetic divergence is low compared with a mean F_{ST} of 0.048 for 23 other bird species based on allozyme data (Evans 1987), but it agrees with the previous allozyme study of Wood Storks ($F_{ST} = 0.019$; Stangel et al. 1990). Studies of population structure in White Ibises (*Eudocimus albus*) from the southeastern United States also revealed low levels of genetic variability and differentiation, although compared with Wood Storks, individuals of this species are considerably more mobile, and breeding colonies are more ephemeral (Stangel et al. 1991).

Obtaining reliable estimates of gene flow among populations is one of the most important (albeit difficult) problems in conservation biology (Varvio et al. 1986, Avise 1994). Values of F_{ST} measure the extent to which species are organized into subpopulations (Wright 1931, 1965). If populations are in selection-mutation equilibrium, genetic differentiation among subpopulations is related to genetic drift and the magnitude and direction of gene flow. Therefore, levels of gene flow can be estimated based on the degree of genetic differentiation. For example, only a single migrant per generation is necessary to prevent differentiation among subpopulations by genetic drift when gene flow among subpopulations is random ("island model"; Wright 1965). Therefore, assuming an island model with a mean F_{ST} of

0.015, 16.4 migrants (N_m) per generation would maintain the observed level of intercolony genetic differentiation. Stangel et al. (1990) obtained a similar value ($N_m = 12.9$) based on an allozyme analysis of Florida Wood Storks. These relatively large estimates of N_m indicate that (1) colonies are of recent origin and have not had sufficient time to become genetically differentiated, or (2) levels of gene flow have been and remain high.

Conservation implications.—Similar to the results of Stangel et al. (1990), our study revealed low levels of genetic variation within and among Wood Stork colonies. Stangel et al. (1990) concluded that large-scale colony shifts, in concert with insufficient time for Wood Stork numbers to increase significantly, were possible explanations for the lack of genetic variation and differentiation that they detected. A third possibility that cannot be excluded is that low levels of genetic variation resulted from limited genetic variability in the founding population of Wood Storks that colonized the southeastern United States. Leberg (1993) demonstrated that allelic diversity of founders influenced the overall levels of genetic variation and success of resulting populations of mosquitofish (*Gambusia holbrooki*) more than either founder heterozygosity or the number of stocks from which the founders were taken. Evidence to support the hypothesis that a founder effect is related to low allelic diversity and heterozygosity in Wood Storks is the observation that even though the breeding population in the Southeast declined beginning in the 1930s, the lowest estimated number of breeding individuals was about 10,000, which should represent a large enough sample to maintain a significant proportion of the genetic variation present in the population prior to the decline (if such variation existed). Moreover, because considerable error exists in Wood Stork population estimates (Rodgers et al. 1995), the estimated colony sizes probably are conservative, and actual numbers of individuals may be many times higher than reported. Finally, due to many factors, census population size frequently is much larger than effective population size (N_e), which determines the rate at which genetic variation is lost (Wright 1931, Kimura and Crow 1963).

Based on single-locus and multilocus microsatellite analyses, Wood Stork colonies in the southeastern United States are characterized by

low levels of allelic diversity and heterozygosity and no significant intercolony genetic structure. In addition, the probability of randomly selecting from a colony two individuals with identical genotypes at all four microsatellite loci is similar to the probability of selecting two individuals with identical genotypes from the entire population. One possible interpretation of these results is that annual pair bonds are formed among individuals from different colonies. Such a strategy of outbreeding simultaneously would reduce the rate of loss of genetic variability and increase the effective population size. There is no evidence that coastal colonies are significantly different than inland colonies. The significance of these findings with regards to Task 3.2 of the Wood Stork recovery plan (USFWS 1996) is that Wood Storks in the southeastern United States should be managed as a single randomly breeding population, as proposed by Stangel et al. (1990).

Future studies should be conducted using additional microsatellite loci and other highly variable nuclear loci to obtain a more detailed estimate of genetic diversity in Wood Stork populations in the southeastern United States. The identification of other loci that exhibit higher levels of variability and allelic diversity could prove valuable for identification of source and sink populations, which are critical to the recovery of Wood Storks in the United States.

Finally, a critical next step to understanding levels of genetic variability in Wood Storks is to compare colonies from the United States with colonies throughout Central and South America. Such a comparison would help determine whether the observed low levels of genetic variability and lack of population differentiation among Wood Stork colonies in the United States are characteristic of all Wood Stork colonies. Genetic studies of the nine-banded armadillo (*Dasypus novemcinctus*) suggest that armadillos from Brazil are genetically more variable than those from North America (Loughry et al. 1998). Similar to Wood Storks, this species of armadillo occurs over a broad latitudinal range in the New World, with its primary distribution extending through South and Central America and the northern limit of its range in the southern and southeastern United States. If comparative analyses indicate that Wood Storks in other portions of their range are not characterized by low levels of genetic variability,

this information could prove useful to evaluate which populations should serve as sources of added genetic variability if future population reductions in the United States should make such actions advisable, as was done for the Florida panther (*Felis concolor coryi*; O'Brien et al. 1996).

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