Genetic Variation and Population Structure of the Florida Wood Stork

PETER W. STANGEL,[1] JAMES A. RODGERS JR.,[2] AND A. LAWRENCE BRYAN[1]
[1]*Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802 USA, and*
[2]*Wildlife Research Laboratory, Florida Game and Fresh Water Fish Commission, Gainesville, Florida 32601 USA*

The Wood Stork (*Mycteria americana*) is a colonial wading bird of the tropical and lower subtropical zones of the Americas. In Florida, Wood Storks are nonvisual, tactile feeders and require high densities of small aquatic organisms in shallow water for foraging (Kahl 1964). These conditions occur when prey are concentrated as water levels drop during the annual dry season (Kahl 1964, Kushlan et al. 1975). Colony formation in Wood Storks is correlated with the onset of these hydrologic conditions, and successful nesting requires the continuation of these conditions for foraging (Kahl 1964, Kushlan et al. 1975).

Yearly fluctuations and long-term alterations of the hydrologic regime result in abandonment of some colony sites. Nesting records indicate that although storks exhibit colony-site tenacity, most—if not all—colonies are transitory in nature (Ogden and Patty 1981, Kushlan and Frohring 1986). Censuses also have documented gradual site shifts among regions (Kushlan and Frohring 1986, Ogden et al. 1987), which implies that following colony abandonment, adult storks disperse widely to renest in more favorable areas.

Although large-scale shifts of storks among areas have been documented (Kushlan and Frohring 1986, Ogden et al. 1987), relatively little is known about the dispersal and fate of adult storks following colony abandonment. These individuals move to areas where favorable foraging conditions exist, but it is unclear where or how far they move, whether or not they reattempt nesting, and if pair bonds remain intact. Without this information, it is impossible to assess the effects of colony-site shifts on stork population structure. Shifts of large numbers of individuals from one site to another could have a potentially dramatic effect on population structure. If breeding individuals are interchanged among colonies, then population shifts would represent gene flow on a massive scale. Large-scale movement of individuals would likely swamp evolutionary processes creating population structure (e.g. selection, random genetic drift) and reduce differentiation among colonies. We collected allele frequency data from Florida colonies to estimate levels of heterozygosity, to examine patterns of population structure, and to estimate levels of gene flow.

We sampled from 15 colonies in 1985 and 1986 (Table 1, Fig. 1). Two growing, centrally located primary feathers (one from each wing) were plucked, placed in plastic vials, and frozen in liquid nitrogen within one hour of collection. Samples were stored in an ultra-cold freezer (−76°C). One individual from each nest was sampled, and sample sizes reflect the number of nests sampled within colonies. Colony sizes at the time of sampling ranged from 76–592 nests. Our samples represented 5–24% of all nests present ($\bar{x}$ = 12%).

Pulp was squeezed from the feather shaft and homogenized with 5–6 ml of 0.01 M Tris-0.001 M EDTA pH 7.0 buffer solution. Gels of 11–12% starch were run overnight. General staining followed Selander et al. (1971) and Harris and Hopkinson (1976). Buffer conditions for 20 presumptive gene loci are provided in Table 2. Presumptive loci were numbered from anode to cathode. Allozymes were designated alphabetically in order of relative mobility from anode to cathode, with the letter "C" chosen to represent the most common allele.

We used the statistical package BIOSYS-1 (Swofford and Selander 1981) to analyze allele frequencies, genetic variability measures (heterozygosity, mean number of alleles per locus, percent polymorphic loci), Chi-square deviation from Hardy-Weinberg proportions, Nei's (1978) and Rogers' (1972) genetic distance, and *F*-statistics (Nei 1977, Wright 1978). Heterozygosity data were arcsine square-root transformed before analysis of variance (ANOVA) to test for differences among populations. We used a Chi-square test with Levene's (1949) correction for small sample size to detect departure from Hardy-Weinberg proportions. For comparative purposes we present two measures of genetic distance (Rogers 1972, Nei 1978) that differ in their assumptions and methodologies. A dendrogram of the genetic relationships among colonies was generated from the matrix of Rogers' distance values. A permutational Mantel test (1967, Sokal 1979) was used to compare matrices of straight-line geographic and genetic distance for congruence of pattern.

To examine population structure, we used Wright's *F*-statistics (Wright 1978). The among-population component of genetic variance, F_{ST}, measures the extent to which species are organized into subpopulations or demes. F_{ST}-values ranged from 0 (indicating lack of differentiation) to 1 (suggesting fixation of alternate alleles and complete differentiation). F_{IS} and F_{IT} measure heterozygote deficiency or excess within subpopulations and the total population, respectively, and are commonly used as inbreeding indices. Both values range from −1 to +1, with positive values indicating heterozygote deficiency (e.g. as may occur from inbreeding). Precise interpretation of *F*-statistics required detailed knowledge about the breeding structure of the species examined. Because this information is usually lacking, inferences about pop-

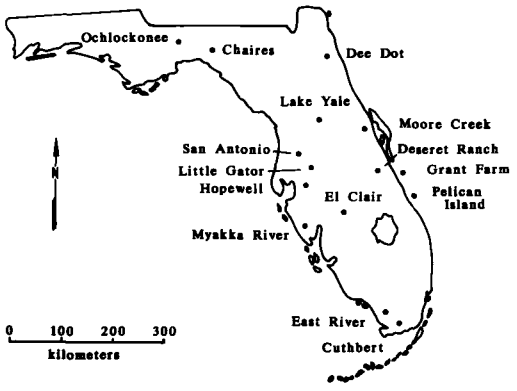

Fig. 1. Location of Wood Stork colonies sampled for genetic survey.

ulation structure based on *F*-statistics are made cautiously. We used Slatkin's (1981) technique for qualitative assessment of gene flow and estimated Nm (N = deme size; m = migration rate among demes) from F_{ST} (Wright 1943).

We resolved 16 enzymes coding for 20 presumptive gene loci from 396 nestlings. Eleven loci (68%) were monomorphic across all populations. Four of the nine polymorphic loci were only slightly polymorphic, with allele frequencies <0.05 (Table 2). There was no convincing evidence for deviation from Hardy-Weinberg proportions. Heterozygosity estimates within colonies ranged from 7.7 to 10.6% ($\bar{x} \pm$ SE = 9.3 ± 4.1%) and did not differ significantly among colonies (Table 1). Mean number of alleles per locus and percent polymorphic loci were uniform, with species means of 1.5 ± 0.2% and 45%, respectively (Table 1). Mean F_{ST} in the Wood Stork was 0.019, which is statistically significant from zero. Mean F_{IS} and F_{IT} were negative, indicating a slight trend for heterozygote excess (Table 3).

Genetic distances among colonies were very small. Of 115 among-colony comparisons, 86 had a Nei's distance of 0, with a mean of 0.0004 and range of 0.000–0.005. Rogers' distance ranged from 0.007 to 0.028 ($\bar{x}$ = 0.017). The permutational Mantel test indicated no significant relationship between straight-line geographic distance and genetic distance. Allele frequencies differed significantly among colonies at the Icd-1 locus only. Two "private polymorphisms" (allele detected in only one population) were detected, both at the Gpi locus (Table 2).

Slatkin's qualitative technique (1981) indicates high levels of gene flow among colonies. The estimated number of migrants per generation based on *F*-statistics was Nm = 12.9. This suggests that either historical levels of gene flow were high, or that colonies are of recent origin and thus not genetically differentiated, or that current levels of gene flow are high. These cannot be differentiated with indirect estimates of gene flow like that of Wright.

Heterozygosity is higher in the Wood Stork than in other Ciconiiformes we have examined for the same loci (unpubl. data) and for birds in general (Evans 1987). No historical estimates of heterozygosity are available for comparison, but current high levels imply that genetic variation in the Wood Stork has not been lost because of severe population bottlenecks.

The small F_{ST} in the Wood Stork indicates that only 1.9% (0.019 × 100) of the total variance detected can be attributed to differences among colonies. The remainder is present within individual colonies. Evans (1987) reported a mean F_{ST} of 0.048 for 23 bird species. Genetic distances among colonies were small and comparable to estimates from other bird studies (Barrowclough 1980, mean Nei's D = 0.0024). The largest Nei's D recorded between colonies was only 0.005,

TABLE 1. Genetic variability for 20 loci in 15 colonies of the Wood Stork. Sample sizes are in parentheses.

Colony	No. of alleles/locus ($\bar{x}$ ± SE)	Percentage of loci polymorphic[a]	Mean heterozygosity (direct count)
1. Ochlockonee (30)	1.4 ± 0.1	25.0	0.102 ± 0.044
2. Chaires (33)	1.4 ± 0.1	20.0	0.094 ± 0.044
3. Dee Dot (30)	1.4 ± 0.1	20.0	0.089 ± 0.039
4. Lake Yale (21)	1.3 ± 0.1	20.0	0.106 ± 0.051
5. Moore Creek (30)	1.4 ± 0.1	20.0	0.089 ± 0.041
6. San Antonio (27)	1.3 ± 0.1	20.0	0.091 ± 0.045
7. Little Gator (17)	1.3 ± 0.1	25.0	0.094 ± 0.042
8. Deseret Ranch (19)	1.3 ± 0.1	25.0	0.087 ± 0.039
9. Grant Farm (30)	1.3 ± 0.1	20.0	0.077 ± 0.039
10. Hopewell (24)	1.3 ± 0.1	20.0	0.081 ± 0.038
11. Pelican Island (31)	1.4 ± 0.1	25.0	0.104 ± 0.043
12. El Clair (28)	1.4 ± 0.1	25.0	0.098 ± 0.041
13. Myakka River (30)	1.3 ± 0.1	20.0	0.092 ± 0.043
14. East River (16)	1.3 ± 0.1	20.0	0.098 ± 0.048
15. Cuthbert (30)	1.4 ± 0.1	20.0	0.091 ± 0.040

[a] A locus was considered polymorphic if the frequency of the most common allele did not exceed 0.95.

TABLE 2. Allele frequencies and electrophoretic conditions for polymorphic protein loci in 15 colonies of the Wood Stork.[a] See Table 1 for colony names; Fig. 1 for locations.

EC number[b]	Enzyme locus (acronym)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Buffer (ph)	$\bar{x}$
1.1.1.42	Isocitrate dehydrogenase (Icd-1)																Amine citrate 6.1	
	C	0.500	0.591	0.583	0.595	0.450	0.426	0.412	0.632	0.450	0.750	0.452	0.589	0.450	0.500	0.472		0.522
	D	0.500	0.409	0.417	0.405	0.550	0.574	0.588	0.368	0.550	0.250	0.548	0.411	0.550	0.500	0.528		0.478
1.1.1.42	Isocitrate dehydrogenase (Icd-2)																Tris maleate 7.4	
	B	0.067	0.000	0.037	0.024	0.034	0.000	0.088	0.053	0.000	0.042	0.081	0.054	0.000	0.031	0.016		0.033
	C	0.933	1.000	0.963	0.976	0.966	1.000	0.912	0.947	1.000	0.958	0.919	0.946	1.000	0.969	0.984	15	0.967
1.1.1.43	Phosphogluconate dehydrogenase (Pgd)																Tris citrate 8.0	
	B	0.017	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.033		0.006
	C	0.983	1.000	1.000	1.000	0.983	1.000	1.000	1.000	1.000	1.000	0.984	1.000	1.000	1.000	0.967		0.994
2.4.2.1	Nucleoside phosphorylase (Nsp)																Tris maleate 7.4	
	B	0.383	0.364	0.400	0.350	0.362	0.389	0.412	0.342	0.350	0.354	0.397	0.446	0.433	0.333	0.468		0.389
	C	0.617	0.636	0.600	0.650	0.638	0.611	0.588	0.658	0.650	0.646	0.603	0.554	0.567	0.667	0.532		0.611
2.7.3.2	Creatine kinase (Ck-2)																Tris maleate 7.4	
	C	1.000	0.985	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.964	1.000	1.000	1.000		0.996
	D	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.036	0.000	0.000	0.000		0.004
3.4.11.4	Tripeptide aminopeptidase[c] (Tri)																Tris citrate 8.0	
	C	0.783	0.818	0.800	0.690	0.767	0.722	0.706	0.763	0.817	0.792	0.726	0.732	0.817	0.656	0.790		0.766
	D	0.150	0.136	0.167	0.310	0.217	0.185	0.235	0.237	0.150	0.208	0.226	0.196	0.100	0.313	0.194		0.193
	E	0.067	0.045	0.033	0.000	0.017	0.093	0.059	0.000	0.033	0.000	0.048	0.071	0.083	0.031	0.016		0.042
5.3.1.8	Mannose phosphate isomerase (Mpi-1)																Tris citrate 8.0	
	C	0.767	0.773	0.867	0.833	0.900	0.815	0.794	0.816	0.917	0.833	0.767	0.804	0.783	0.906	0.839		0.826
	D	0.233	0.227	0.133	0.167	0.100	0.185	0.206	0.184	0.083	0.167	0.233	0.196	0.217	0.094	0.161		0.174

TABLE 2. Continued.

EC number[b]	Enzyme locus (acronym)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Buffer (ph)	F
5.3.1.9	Glucosephosphate isomerase (Gpi-1)																Tris citrate 8.0	
	B	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.001
	C	1.000	0.985	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.984	1.000	1.000	1.000	1.000		0.997
	D	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000		0.001
5.4.2.2	Phospho-glucomutase (Pgm)																Tris citrate 8.0	
	C	1.000	1.000	0.967	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		0.997
	D	0.000	0.000	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.003

[a] The following loci were monomorphic in all individuals assayed (EC numbers in parentheses): Lactate dehydrogenase-1 (1.1.1.27), Malate dehydrogenase-1 & 2 (1.1.1.37), Malic enzyme-1 (1.1.1.40), Superoxidase dismutase-1 (1.15.1.1), Creatine kinase-1 (2.7.3.2), Adenylate kinase-1 & 2 (2.7.4.3), Acid phosphatase (3.1.3.2), Leucine aminopeptidase (3.4.11), Glucosephosphate isomerase-2 (5.3.1.9)-2.

[b] Enzyme Commission number recognized by International Union of Biochemistry (1984).

[c] Substrate for tripeptide aminopeptidase was leucylglycylglycine.

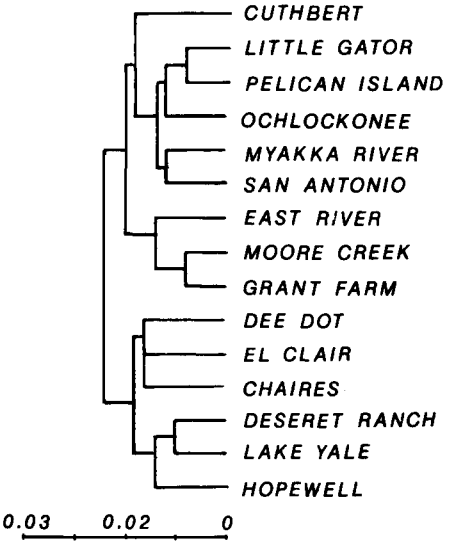

Fig. 2. Phenogram derived from matrix of Rogers' genetic distance.

and almost 75% of intercolony comparisons had a Nei's D of zero. The greatest D values occurred between the Hopewell colony and some (Grant Farm, Pelican Island, Myakka River, San Antonio) geographically proximate colonies. Small genetic distances among colonies necessitate cautious interpretation of cluster patterns in the dendrogram. We did not determine any biological meaning for the two large groupings in the dendrogram (Fig. 2), but the five colonies in coastal habitat (marine-estuarine vegetation such as mangrove) clustered together.

Small genetic differences among Florida Wood Stork colonies do not necessarily indicate a lack of genetic differences or population structure. With protein electrophoresis, only a tiny fraction of genes present in one portion of the genome is examined. More sensitive genetic techniques might reveal greater genetic differences among colonies. That protein electrophoresis can often detect differences among populations suggests to us, however, that genetic differences among stork colonies are likely small.

Several factors including uniform stabilizing selection, slowed rate of molecular evolution, recent colonization, and a high level of gene flow could be responsible for low protein divergence (see Zink 1986 for more complete discussion of these factors). Identification of causative factors is difficult because the observed patterns are likely the result of interaction among several processes, and the intensity of this interaction may have changed during the evolutionary history of the stork in Florida. We suggest, however, that recent colonization and high levels of gene

TABLE 3. Summary of *F*-statistics at all polymorphic loci in nestling Wood Storks.

Locus	F_{IS}	F_{IT}	F_{ST}
Lgg	−0.285	−0.263	0.017
Gpi-1	−0.016	−0.002	0.014
Pgm	−0.034	−0.002	0.031
Nsp	0.025	0.031	0.006
Ck-2	−0.030	−0.003	0.026
Icd-1	−0.157	−0.118	0.034
Icd-2	−0.061	−0.036	0.024
Mpi-1	0.076	0.091	0.017
Pgd	−0.024	−0.006	0.018
$\bar{x}$	−0.091	−0.070	0.019

flow contribute to low differentiation among Wood Stork colonies in Florida.

Recent colonization of Florida may not have permitted sufficient time for protein differentiation to occur in storks. Fossil records suggest that Wood Storks have been present in Florida at least since the late Pleistocene, ca. 21,000 yr ago (Becker 1985). The Wood Stork's distribution is closely tied to hydrologic conditions, and Florida's geological history has been shaped largely by sea-level changes during the late Cenozoic (Webb 1974). Glacial advances and retreats during this period resulted in large changes in Florida's peninsular land mass (Swift et al. 1986). Colonies located in coastal areas would have shifted periodically in response to sea-level changes. Sea-level changes also may alter inland groundwater levels (Webb 1974), affecting colonies located in freshwater areas. Recolonization of Florida by current vegetational types has occurred during the post-Wisconsin warming period, beginning ca. 18,000 yr ago (Gleason 1974). Long (1974) estimated the age of South Florida vegetation to be ca. 3,000–5,000 yr at most, which implies that current colony distributions are quite recent.

High levels of gene flow among stork colonies may also be a primary factor to reduce genetic divergence. Long-term censuses indicate that although storks tend to return to traditional sites year after year, there is no indication that they are attached to any one site (Ogden and Patty 1981, Kushlan and Frohring 1986). For example, Ogden et al. (1987) record 71 sites used by storks over the last four decades, only 23–47 of which were used in any one period. Only 8 sites were used continuously. Similarly, Rodgers et al. (1987) documented substantial intercolony ($cv = 73.1$–101.6%) and intracolony ($cv = 11.3$–158.9%) variation in size, indicating considerable fluctuation in the number of nesting pairs at particular sites. A decrease in the number of nesting pairs is often associated with increased counts in other areas (Kushlan and Frohring 1986, Ogden et al. 1987). This implies that after colony abandonment, adults move to established or new sites to attempt renesting. One dramatic example of this phenomenon is the 132-km shift northward from southern to central Florida of the stork's geographic center of breeding (Ogden et al. 1987). This shift is apparently in response to unfavorable water-control programs at traditional southern Florida colonies or their associated foraging areas. Coincident with the shift northward was an increase in the number of nesting pairs from 0 to 605 (in 1985) in Georgia and South Carolina. Historical records also indicate the periodic expansion and contraction of nesting storks into coastal states between Texas and South Carolina (Ogden et al. 1987).

We suggest that the lack of genetic differentiation among colonies may result from interbreeding of storks from different areas after site shifts. Gene flow, as distinguished from dispersal or migration, requires the movement and incorporation of alleles (rather than individuals) from one area to another (Rockwell and Barrowclough 1987). To accomplish gene flow, an immigrant or its offspring must successfully breed with a resident in the new area. In Wood Storks this means that after site shifts, individuals from different colonies come together to breed. If colonies moved intact from one area to another, then gene flow would not occur, and genetic differences might accrue. Studies of marked storks are needed to confirm mixing of gene pools from different regions.

Kushlan and Frohring (1986) did not consider colonies to be natural population divisions, because they found no indication that Wood Storks are restricted to a single colony. Ogden et al. (1987) concluded that the Florida Wood Storks represent a single population with no evidence of discrete subpopulations. The lack of genetic differentiation among colonies revealed by our survey supports these earlier observations.

We thank those individuals, agencies, and companies that allowed us access to the colony sites under their jurisdiction: J. E. Davis, Golden Gem Growers Inc., Merritt Island National Wildlife Refuge, Pelican Island National Wildlife Refuge, B. Tomberg, Everglades National Park, Deseret Ranch, El Clair Ranch, Hopewell Phosphate Co., and S. Grossenbacker. Many individuals assisted in the collection of tissue samples, especially K. C. Williams, R. D. Bjork, Capt. J. West, and S. T. Schwikert. P. Dixon assisted with statistical analysis. A. Capparella, M. C. Coulter, J. A. Kushlan, J. M. Novak, J. Ogden, and M. Romano helped with earlier drafts of the manuscript. J. Hinton patiently processed and reprocessed the manuscript. Research and manuscript preparation were supported by contract DE-AC09-76SROO-819 between the U.S. Department of Energy and the University of Georgia's Savannah River Ecology Lab.

LITERATURE CITED

BARROWCLOUGH, G. F. 1980. Genetic and phenotypic differentiation in a wood warbler (Genus *Dendroica*) hybrid zone. Auk 97: 655–668.

BECKER, J. J. 1985. A Late Pleistocene (Wisconsinan) avifauna from West Palm Beach, Florida. Bull. Br. Ornithol. Club 105: 37–40.

EVANS, P. G. H. 1987. Electrophoretic variability of gene products. Pp. 105–162 *in* Avian genetics: a population and ecological approach (F. Cooke and P. A. Buckley, Eds.). Orlando, Florida, Academic Press.

GLEASON, P. J. 1974. Environments of south Florida: present and past. Mem. 2. Miami Geol. Soc., Miami, Florida.

HARRIS, H., & D. A. HOPKINSON. 1976. Handbook of enzyme electrophoresis in human genetics. New York, Elsevier.

KAHL, M. P. 1964. Food ecology of the Wood Stork (*Mycteria americana*) in Florida. Ecol. Monogr. 34: 97–117.

KUSHLAN, J. A., & P. C. FROHRING. 1986. The history of the southern Florida Wood Stork population. Wilson Bull. 98: 368–386.

———, J. C. OGDEN, & A. L. HIGER. 1975. Relation of water level and fish availability to Wood Stork reproduction in the southern Everglades, Florida. U.S. Geol. Surv. Open File Rep. 75-434, Tallahassee, Florida.

LEVENE, H. 1949. On a matching problem arising in genetics. Ann. Math. Stat. 20: 91–94.

LONG, R. W. 1974. Origin of the vascular flora of south Florida. Pp. 28–34 *in* Environments of south Florida: present and past (P. J. Gleason, Ed.). Mem. 2. Miami Geol. Soc., Miami, Florida.

MANTEL, N. 1967. The detection of disease clustering and a general regression approach. Cancer Res. 27: 209–220.

NEI, M. 1977. F-statistics and analysis of gene diversity in subdivided populations. Ann. Hum. Genet. 41: 225–233.

———. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583–590.

OGDEN, J. C., D. A. MCCRIMMON JR., G. T. BANCROFT, & B. W. PATTY. 1987. Breeding populations of the Wood Stork in the southeastern United States. Condor 89: 752–759.

———, & B. W. PATTY. 1981. The recent status of the Wood Stork in Florida and Georgia. Pp. 97–103 *in* Proceedings of the second nongame and endangered wildlife symposium (R. R. Odom and J. W. Guthrie, Eds.). Georgia Dep. Nat. Res., Game and Fish Division.

ROCKWELL, R. F., & G. F. BARROWCLOUGH. 1987. Gene flow and the genetic structure of populations. Pp. 223–255 *in* Avian genetics: a population and ecological approach (F. Cooke and P. A. Buckley, Eds.). Orlando, Florida, Academic Press.

RODGERS, J. A., JR., A. S. WENNER, & S. T. SCHWIKERT. 1987. Population dynamics of Wood Storks in north central Florida, USA. Colon. Waterbirds 10: 151–156.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Univ. Texas Publ. 7213: 145–153.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, & J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Pp. 49–90 *in* Studies in genetics, vol. 6. Univ. Texas Publ. 7103.

SLATKIN, M. 1981. Estimating levels of gene flow in natural populations. Genetics 99: 323–335.

SOKAL, R. R. 1979. Testing statistical significance of geographic variation patterns. Syst. Zool. 28: 227–232.

SWIFT, C. C., C. R. GILBERT, S. A. BORTONE, G. H. BURGESS, & R. W. YERGER. 1986. Zoogeography of the freshwater fishes of the southeastern United States: Savannah River to Lake Pontchartrain. Pp. 213–265 *in* The zoogeography of North American freshwater fishes (C. H. Hocutt and E. O. Wiley, Eds.). New York, John Wiley & Sons.

SWOFFORD, D. L., & R. B. SELANDER. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. 72: 281–283.

WEBB, S. D. 1974. Pleistocene mammals of Florida. Gainesville, Univ. Presses Florida.

WRIGHT, S. 1943. Isolation by distance. Genetics 28: 114–138.

———. 1978. Evolution and genetics of populations, vol. 4. Variability within and among populations. Chicago, Univ. Chicago Press.

ZINK, R. M. 1986. Patterns and evolutionary significance of geographic variation in the Schistacea group of the Fox Sparrow (*Passerella iliaca*). Ornithol. Monogr. 40. Washington, D.C., Am. Ornithol. Union.

Received 30 June 1989, accepted 25 February 1990.