SEASONAL MIGRATION AND GENETIC POPULATION STRUCTURE IN HOUSE WRENS[1]

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Abstract. Neotropical migrant birds have undergone significant changes in population size, due in part to alterations in the landscape in their breeding range. Some alterations have resulted in the isolation of areas containing optimal habitat for breeding. Isolation between habitat fragments could reduce gene flow between populations, which might result in loss of genetic variation due to genetic drift. To test whether isolation due to distance between populations may affect migratory birds as much as sedentary birds, we used four microsatellite loci as genetic markers to compare gene flow and population structure in migratory and sedentary House Wrens (*Troglodytes aedon* and *T. musculus,* respectively). If migratory behavior enhanced gene flow, we expected to find that populations of migratory birds were genetically more similar than populations of sedentary birds, and that gene flow declined more rapidly with distance in sedentary than in migratory populations. Blood samples were collected from 18–25 migratory House Wrens at each of six sites in Ohio separated by distances from 25 to over 300 km, and from 16–20 sedentary House Wrens at each of six sites in Costa Rica, also at distances up to 350 km. We used heterologous microsatellite primers to obtain estimates for R_{ST} (population subdivision) and Nm (number of immigrants per generation) in relation to distance between pairs of populations. In the migratory populations, Mantel permutational tests showed no effect of distance on R_{ST} or Nm at distances between 25 and 300 km. In the sedentary birds, R_{ST} increased and Nm decreased significantly as distance between populations increased from 25 to 300 km. F_{ST} values were not different from those obtained using Slatkin's (1995) R_{ST} statistics. These results are consistent with our hypothesis that migratory behavior enhances gene flow.

Key words: gene flow, House Wrens, migratory birds, population structure, sedentary birds, Troglodytes aedon, Troglodytes musculus.

INTRODUCTION

Neotropical migrant birds have shown significant variation in numbers in the last few decades; some species have decreased enough to be considered threatened, others appear stable, whereas others have shown dramatic increases (Hagan and Johnston 1992, James et al. 1996). Populations may fluctuate in size as a result of changes in the physical environment (Flather and Sauer 1996, Boulinier et al. 1998) or other factors, such as increased competition and predation from introduced species (Fritts and Rodda 1998, Russell et al. 1998), and the level of stability typical of a particular environment (Tewksbury and Martin 1998). These factors may affect birds in the breeding range, wintering range, or during their seasonal long-distance flights (Hagan et al. 1992, Sutherland 1998). One concern is that increasing fragmentation of habitat on the breeding grounds may result in increased isolation of breeding habitat patches, thereby inhibiting dispersal and limiting gene flow between sites. Reduced gene flow may promote loss of genetic variation within breeding sites due to genetic drift, which may affect fitness and population persistence (Frankham 1996). The capacity to travel long distances does not necessarily make migratory birds better colonists of new areas (Bohning-Gaese et al. 1998). Nonetheless, isolation of populations within an established range might not be expected of organisms that are capable of crossing wide expanses of inhospitable habitat during their sea-

sonal movements. Because of the high mobility of migratory birds, high levels of gene flow have been assumed (Rockwell and Barrowclough 1987). Based on data using protein electrophoresis, Barrowclough (1980) considered that the entire range of a migratory species might form a single, panmictic population. In contrast, return rates of some migratory bird species (Brawn and Robinson 1996) indicate that dispersal to new breeding sites may not be as widespread as previously believed; these authors also point out that our present knowledge of the magnitude of dispersal in these birds is inadequate to respond to our current conservation needs. The difficulties involved in the study of dispersal in the field have stimulated its estimation through indirect methods that compare population structure and gene flow with the use of genetic markers. Bohonak (1999) has found that genetic statistics such as Wright's (1951) F_{ST} are generally robust for making inferences about the movements of individuals between sites.

Here, we test the hypothetical relationship between migratory behavior and gene flow by comparing population structure of migratory and sedentary birds with the use of microsatellites as genetic markers. Microsatellites (Tautz 1989) are short, tandemly repeated sequences of nuclear DNA [such as $(CA/GT)_n$ or $(CAT/GTC)_n$] which are characterized by high mutation rates (as high as 10^{-3} per generation) and simple Mendelian mode of inheritance. Their high polymorphism in the number of tandem repeats and their mode of inheritance make them ideal markers for population studies (Ellegren 1992, Queller et al. 1993). This is particularly true for studies focusing on vertebrates (e.g., Wenburg et al. 1998, Gladden et al. 1999, Van Treuren et al. 1999) for which a large number of microsatellite loci are accessible. The detection of size variation in microsatellite alleles among breeding individuals permits the assessment of gene flow: distinguishable patterns of allelic diversity can be observed, as size mutations occur independently in each population and are inherited in Mendelian fashion, and genetic drift changes allele frequencies in isolated populations. As in studies that use protein polymorphisms as markers (Wright 1951; see Rockwell and Barrowclough 1987 for references on avian species), population structure is detected through the determination of the presence, absence, or differences in frequencies of particular alleles among populations. High

gene flow translates into shallow population subdivision (high genetic similarity between populations); lower gene flow results in deeper population substructuring (less similarity between populations).

We compare population structure in two closely related members of the passerine species group, the House Wren, *Troglodytes* spp., whose complete range includes most of the American continents (Fig. 1). As an edge/second-growth species, the House Wren is ubiquitous in human-altered landscapes (Skutch 1960, Bent 1964, Ridgely and Tudor 1989). The Northern House Wren (*T. aedon*) is a long-distance migrant; its breeding range covers most of North America, and its wintering range extends from the southern states to southern Mexico (Bent 1964). The migratory Northern House Wren has experienced impressive population increases in its North American range (Hagan et al. 1992, Earnst and Andres 1995). These increases have been attributed to land conversion and agriculturalization, the wrens' aggressive behavior in obtaining nesting sites (White and Kennedy 1997, Hannon and Cotterill 1998) and defending them (Pribil and Picman 1997), and their ability to take advantage of conservation measures directed to other cavity nesters (Purcell et al. 1997). Its southern Central American counterpart (*T. a. musculus,* or *T. musculus* according to Brumfield and Capparella 1996) is a year-round resident in most habitats except the very dry or those above 270 m (Stiles and Skutch 1989). Southern House Wrens share with the North American form the behavioral traits that make them successful (Skutch 1960, Beissinger et al. 1998). Land conversion also has increased the size and the connectivity of the habitat of the Southern House Wren (Sanchez-Azofeifa et al. 1999).

Following the hypothesis that the migratory habit enhances gene flow, it is our expectation that population structure will be shallower (indicating more gene flow) in the migratory northern House Wrens than in the sedentary southern House Wrens. We also expect that in both migratory and sedentary birds, gene flow will decline as distance between populations increases, and that the decline in gene flow will be steeper in sedentary compared to migratory birds.

METHODS

SAMPLING AREAS AND FIELD METHODS

Populations of the migratory Northern House Wren were sampled in Ohio during the 1994

breeding season. Between 18 and 25 individuals were mist-netted at each of six sites located over 300, 150, 80, 40, and 25 km apart (Fig. 1). Blood samples (20–40 μl each) were obtained by puncture of the brachial vein and mixed immediately with 500–700 μl of lysis buffer (100 mM Tris pH 8.0, 100 mM EDTA, 10 mM NaCl, 0.5% SDS; Longmire et al. 1988).

Populations of sedentary Southern House Wrens were sampled in Costa Rica during the breeding season of 1996. In order to obtain sufficient samples within a small geographical radius, wren populations were sampled in the proximity of small towns (5,000–10,000 inhabitants), in which the species tends to be abundant. Six populations were sampled at distances of approximately 300, 150, 80, 40, and 25 km from each other (Fig. 1). Sample sizes were between 16 and 20 individuals per population. Blood samples were collected and preserved in the same manner as the Ohio samples.

LABORATORY PROCEDURES

Purification of total DNA was carried out 1–2 months after blood collection by phenol/chloroform-CIA extraction and dialysis in 1× TNE$_2$ (10 mM Tris-HCl, 10 mM NaCl, 2 mM EDTA). Purity, integrity, and concentration of each DNA sample was determined by spectrophotometry and electrophoresis in 0.8% agarose gels run in 1× TBE. Four polymorphic microsatellite loci (Table 1) were identified and selected by screening House Wren DNA with 25 pairs of PCR (polymerase chain reaction) oligonucleotide primers developed for different passerine species. Three of the loci used in migratory birds (POCC 1, LTMR 6, and Dpmu 16) were the same as those used in the sedentary birds. The fourth locus was different between the migratory and the sedentary forms (FhU 2 and POCC 2, respectively), because no other single locus provided a comparable level of polymorphism in both the migratory and the sedentary forms. Amplification reactions (4–10 μl total volume) were performed in Biometra Uniblock and TrioBlock Automatic Cyclers. We used the touch-down approach, with the following parameters: denaturing was accomplished at 94°C for 30 sec, annealing temperatures were decreased from 52°C to 50°C for 30 sec, each repeated twice, followed by 35 cycles at 49°C for 30 sec each. Product extension was done at 72°C for 30 sec each. PCR products were separated in non-denaturing 7.5% acrylamide/bisacrylamide (29:1) gels in BioRad sequencing rigs run at 25–40 mA for 2–4 hr. The gels were stained with 0.05% ethidium bromide (EtBr) in 1× TBE and thoroughly washed with 1× TBE and distilled water to eliminate unspecifically bound EtBr. The gels were then photographed under ultraviolet light using the IS/1000 Digital Imaging System (Version 2.00, Alpha Innotech Corporation, San Leandro, California) that allows direct estimation of PCR product size by comparison with DNA standards (Gibco-BRL). For the purposes of this study, each allele was identified according to the number of dinucleotides present.

DATA ANALYSES

After determining genotypes for all individuals at the four loci, we calculated heterozygosities per locus per population. The data were then analyzed for linkage using the Expectation-Maximization algorithm (Slatkin and Excoffier 1996), and tested for their compliance with Hardy-Weinberg expectations (Excoffier and Slatkin 1995). Both tests were performed with the genetic analysis package Arlequin (Schneider et al. 1996). No two loci were linked; frequencies at all loci were in equilibrium. Population structure was analyzed based on Michalakis and Excoffier (1996) using the same Arlequin software. We assumed that mutations in microsatellites followed the step-wise mutation model (Ohta and Kimura 1973). We used Slatkin's (1995) statistics R_{ST} (degree of population subdivision) and its mathematically dependent Nm (number of immigrants per generation) for all pairwise comparisons of populations. R_{ST} and Nm between pairs of populations were examined as a function of distance between sites by performing Mantel permutational tests (Mantel 1967, Schnell et al. 1985). Mann-Whitney U-tests were used to compare gene flow among migratory to that among sedentary populations. To evaluate the effect of the assumption of step-wise mutations implicit in Slatkin's R_{ST}, we calculated Wright's (1951) F_{ST} equivalents (as developed by Weir and Cockerham 1984) for all interpopulation comparisons

RESULTS

ALLELIC VARIATION AND HETEROZYGOSITY

Microsatellite genotypes were determined at four loci for 138 individuals from six sites for

FIGURE 1. Sampling sites for migratory and sedentary House Wrens (*Troglodytes* spp.). The shaded area shows the breeding distribution of House Wrens on the American continents.

migratory birds, and at four loci for 116 individuals from six sites for sedentary birds. Average heterozygosities per population (Table 2) ranged between 0.545 and 0.758 in migratory birds, and between 0.240 and 0.609 in sedentary birds. Although recently separated as two different species, at two of the three loci used in common (Table 3), the most common allele(s) per locus were the same or very close in size across sites in migratory and sedentary House Wrens; at the third locus there was a shift toward

much shorter alleles in the sedentary birds. Polymorphism was higher in the migratory birds (37 alleles compared to 29 in the sedentary birds, Fig. 2 and Fig. 3). Among the alleles that were found only in one of the forms, eight were present in the migratory birds and two in the sedentary birds.

PRIVATE ALLELES

Among migratory birds, private alleles (those found in a single population) were present at

TABLE 1. Microsatellite loci used in this study. PCR primer sequences were generously provided by the developers.

Locus name	Origin (species)	Developers
POCC 1	European Warbler (*Phylloscopus*	Bensch et al. (1997)
POCC 2	*occidentalis*), family Sylvidae	
LTMR 6	Long-tailed Manakin (*Chiroxiphia*	McDonald and Potts (1994)
	linearis), family Pipridae	
Dp mu 16	Yellow Warbler (*Dendroica*	Dawson et al. (1997)
	petechia), family Emberizidae	
FhU2	Barn Swallow (*Ficedula hypoleuca*),	Primmer et al. (1996)
	family Hirundinidae	

TABLE 2. Average heterozygosities at four microsatellite loci in migratory and sedentary House Wrens. See Figure 1 for geographical location of populations.

| Population | LOCUS | | | | | Average/ population |
	POCC1	LTMR6	Dpmu16	FhU2	POCC2	
Migratory						
Mahoning	0.250	0.542	0.667	0.710	—	0.542
Medina	0.250	0.833	0.625	0.583	—	0.598
Ashland	0.320	0.640	0.560	0.783	—	0.576
Delaware	0.375	0.542	0.625	0.750	—	0.573
Alum Creek	0.389	0.556	0.667	0.778	—	0.598
Caesar Creek	0.440	0.680	0.680	0.640	—	0.610
Average/locus	0.337	0.632	0.707	0.637		
Sedentary						
Angeles	0.687	0.625	0.437	—	0.687	0.609
Monteverde	0.500	0.550	0.050	—	0.600	0.425
Platanar	0.667	0.250	0.050	—	0.474	0.240
Patarra	0.500	0.700	0.000	—	0.400	0.400
Salitral	0.450	0.450	0.052	—	0.600	0.388
San Vito	0.450	0.250	0.850	—	0.450	0.500
Average/locus	0.542	0.471	0.602	—	0.173	

three of the six sampling sites, with frequencies ranging from 0.02 to 0.07 per population (four unique alleles). Three of the four private alleles were of intermediate size, whereas one was two repeats larger than all others at that locus; three of the four alleles were detected in the two populations at the geographic extremes of our sampling area: Mahoning and Caesar Creek.

In sedentary birds, most of the private alleles were of extreme sizes for each of the loci (Table 3), no matter their geographic location. Private alleles (a total of 11) were present at all six sites, with frequencies between 0.025 and 0.075 per population, except for allele "76" in locus Dpmu 16, which had a frequency of 0.225 in San Vito. At this southernmost site, 4 of the 11 unique alleles were detected, whereas at Angeles, the northernmost site, 3 other alleles were found to be unique.

The presence of private alleles is an indication of limitations in gene flow between populations; their increasing number and frequency would indicate a sharper reduction in gene flow (Slatkin 1985a, 1985b). In a qualitative manner, the sedentary populations of House Wrens appear much less similar to each other than the migratory populations, indicating more gene flow among the populations of migratory birds. This appears especially true for the sedentary House Wrens sampled in San Vito, where one of the private alleles occurs at a high frequency. In both the migratory and the sedentary House Wrens, private alleles were found more frequently at the extremes of our geographical sampling area.

POPULATION STRUCTURE

If migratory behavior enhances gene flow, we expect population subdivision to be stronger

TABLE 3. Allelic variation at four microsatellite loci. Allele sizes are given in number of dinucleotides; in the sedentary birds, private alleles are distributed among populations as follows: Angeles 3, Monteverde 0, Platanar 2, Patarra 1, Salitral 1, San Vito 4. In the migratory birds: Mahoning 1, Medina 1, and Caesar Creek 2.

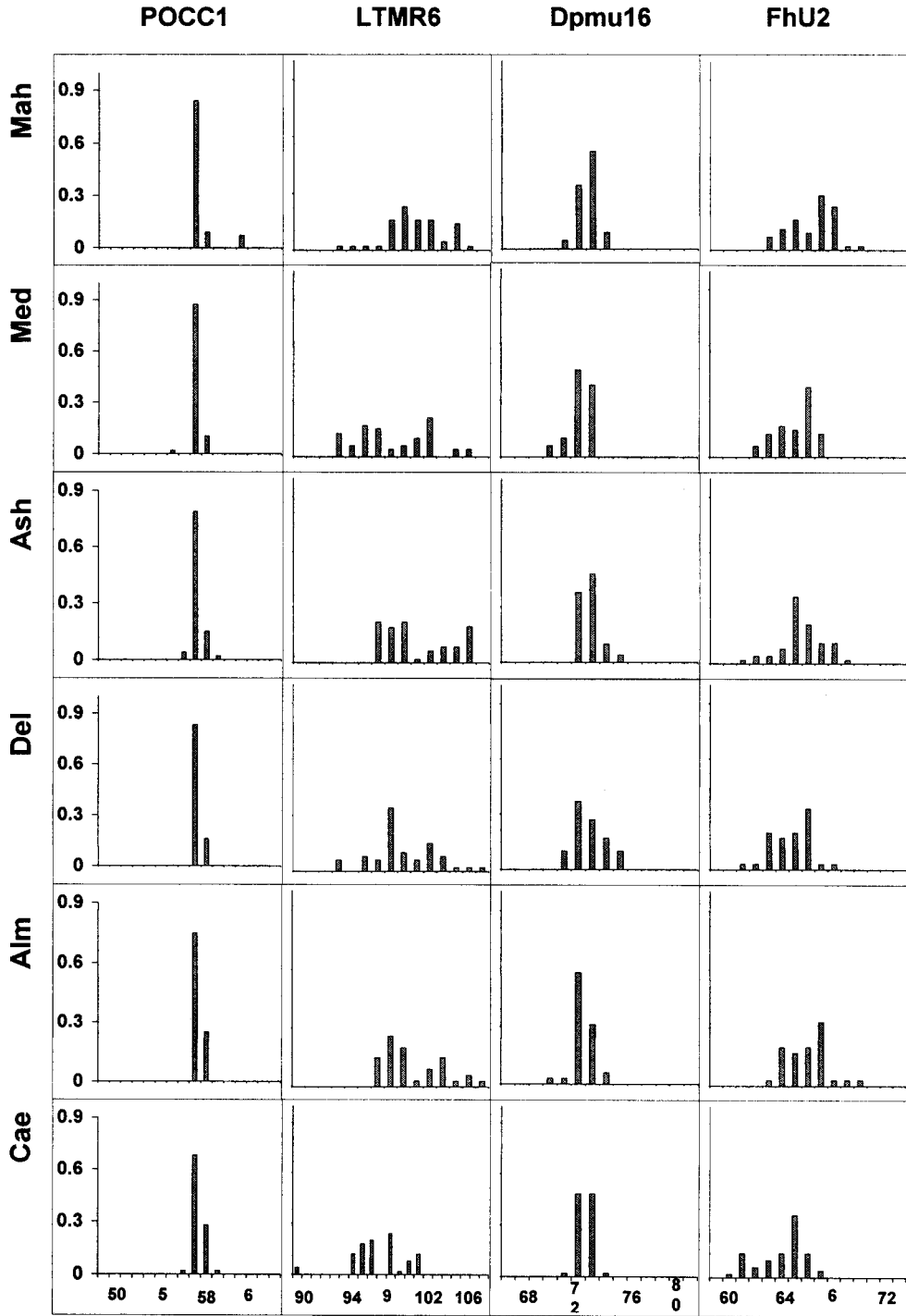| | Migratory birds | | | Sedentary birds | | |
Locus	Number of alleles	Allele size range	Private alleles	Number of alleles	Allele size range	Private alleles
POCC 1	6	56–62	2	4	55–60	1
LTMR6	13	90–104	1	11	94–104	3
Dp mu 16	6	71–76	0	4	74–78	2
POCC 2	—	—	—	12	95–120	5
FhU2	11	61—71	1	—	—	—

FIGURE 2.   Allele frequencies at four microsatellite loci in populations of migratory House Wrens located at distances up to 350 km. Abbreviations for population names are: Mah = Mahoning, Med = Medina, Ash = Ashland, Del = Delaware, Alm = Alum, and Cae = Caesar Creek.
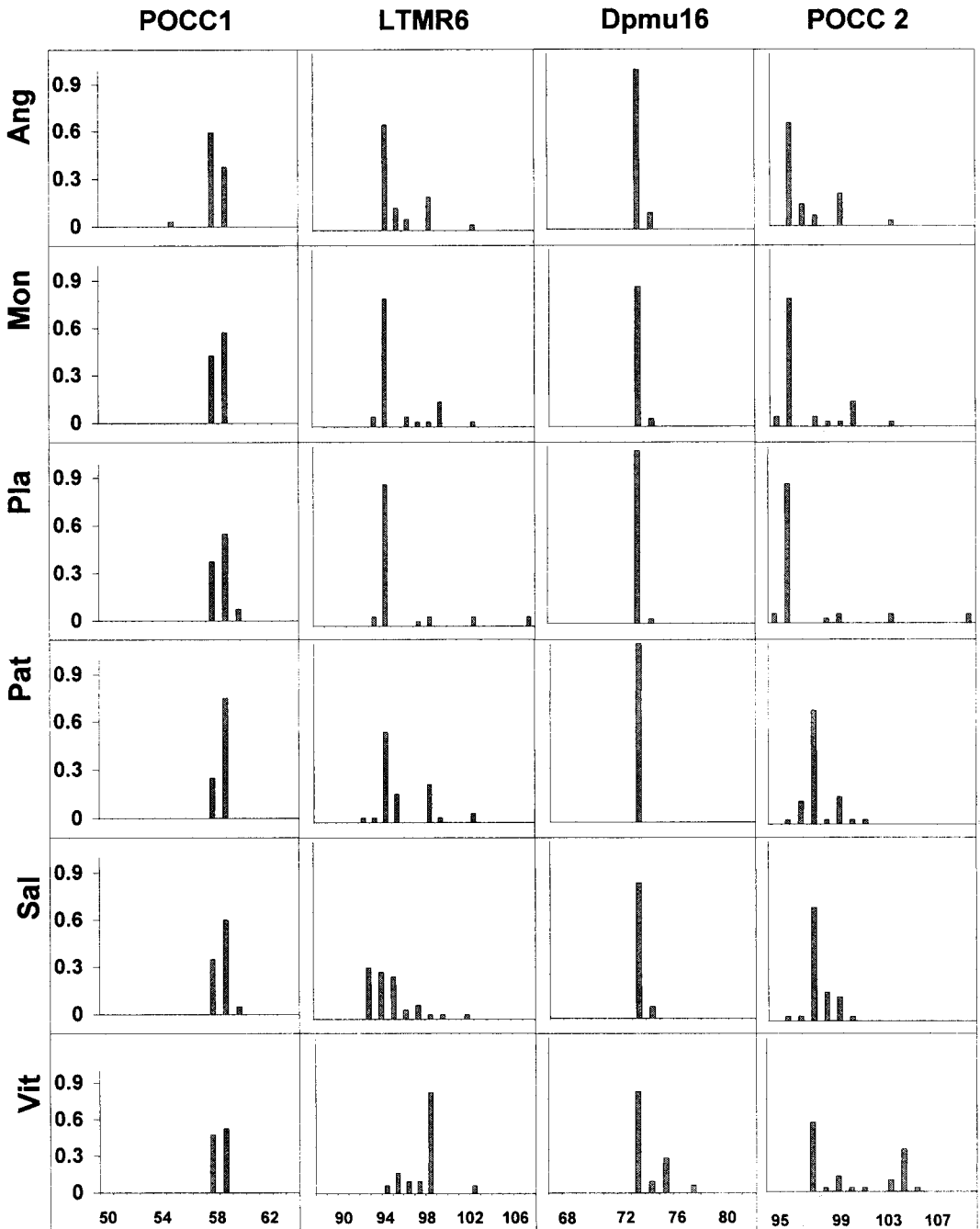
FIGURE 3.   Allele frequencies at four microsatellite loci in populations of sedentary House Wrens located at distances up to 350 km. Abbreviations for population names are: Ang = Angeles, Mon = Monteverde, Pla = Platanar, Pat = Patarra, Sal = Salitral, and Vit = San Vito.

TABLE 4.   Comparison of R_{ST} (bottom) and F_{ST} statistics (top) in migratory House Wrens, and sedentary House Wrens. Pearson correlation coefficient between R_{ST} and F_{ST} in comparisons of migratory populations is 0.994 and among populations of sedentary birds is 0.984.

	Ashland	Delaware	Mahoning	Medina	Alum Creek	Caesar Creek
Migratory						
Ashland		0.00092	0.00259	0.00629	0.00206	0.00173
Delaware	0.00092		0.00227	0.00591	0.00229	0.00091
Mahoning	0.00259	0.00227		0.00634	0.00000	0.00173
Medina	0.00625	0.00587	0.00631		0.00831	0.00501
Alum Creek	0.00206	0.00229	−0.00120	0.00824		0.00387
Caesar Creek	0.00173	0.00091	0.00173	0.00499	0.00385	
	Angeles	Monteverde	Platanar	Patarra	Salitral	San Vito
Sedentary						
Angeles		0.00639	0.00917	0.02126	0.02640	0.02811
Monteverde	0.00635		0.01173	0.02432	0.02625	0.03097
Platanar	0.00909	0.01159		0.00000	0.01189	0.03047
Patarra	0.02082	0.02374	−0.00027		0.00459	0.02320
Salitral	0.02572	0.02558	0.01175	0.00456		0.01482
San Vito	0.02734	0.03004	0.02957	0.02267	0.01461	

(larger R_{ST} or F_{ST}) in sedentary compared to migratory birds. We also expect a steeper positive relationship between R_{ST} (or F_{ST}) and distance between populations, and conversely, a steeper negative relationship between Nm and distance,
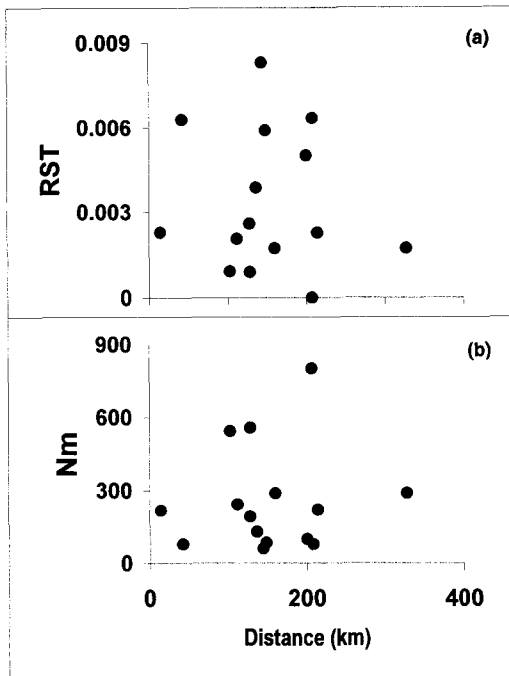

FIGURE 4.   Relationship between distance and (a) population subdivision as R_{ST}, and (b) number of immigrants per generation as Nm in migratory House Wrens.

in sedentary compared to migratory birds. The more immigrants into a population (and the more numerous the sources of these immigrants), the less different this population will be from the surrounding populations. We compared Nm values (which are more familiar than R_{ST} or F_{ST} values to present data on gene flow) between migratory and sedentary populations at less than and more than 150 km, which is the geographic midpoint of distances between our sampling areas. Our expectation is that a significantly larger number of immigrants would be detected in the migratory birds, as would be expected if migratory behavior enhances gene flow. At less than 150 km, the difference in gene flow between migratory ($\bar{x} \pm$ SD: Nm = 234.27 ± 190.42, n = 9) and sedentary (Nm = 70.77 ± 60.12, n = 8) populations was highly significant (Mann-Whitney U = 63.0, P = 0.009). This difference also was highly significant among populations located between 150 and 300 km apart (migratory: Nm = 295.90 ± 262.89, n = 6, sedentary: Nm = 21.16 ± 6.16, n = 7; Mann-Whitney U = 42.0, P = 0.003).

   Migratory House Wrens. R_{ST} values showed a positive direct correlation to F_{ST} values (Table 4) for each of the comparisons between populations for migratory birds (Pearson r = 0.994; 15 population pairs). We found no relationship between distance and degree of population subdivision (Mantel r = −0.334, P = 0.142) at distances as far as 350 km between sites (Fig. 4a). Notice that, contrary to our expectations, population
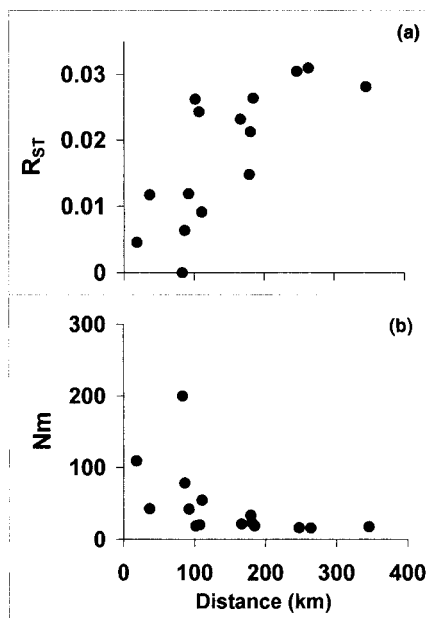
FIGURE 5. Relationship between distance and (a) population subdivision as R_{ST}, and (b) number of immigrants per generation as Nm in sedentary House Wrens.

subdivision has a slight decreasing trend as distance increases. Nm, the number of immigrants per generation (Fig. 4b), is highly variable and unrelated to distance between populations (Mantel $r = 0.407$, $P = 0.08$).

Sedentary House Wrens. R_{ST} values showed a positive direct correlation to F_{ST} values (Table 4) for each of the comparisons between populations (Pearson $r = 0.984$; 15 population pairs). Sedentary House Wrens showed a significant negative relationship between gene flow and distance between populations. At distances from 25 to 350 km, the Mantel permutational test produced $r = -0.422$, $P < 0.04$ for population subdivision (R_{ST}; Fig. 5a) and $r = 0.748$, $P = 0.005$ for the number of immigrants per generation (Nm) between sites (Fig. 5b).

DISCUSSION

If the migratory habit enhances gene flow, we would predict that migratory birds would show shallower population subdivision than sedentary birds. Our data on migratory and sedentary House Wrens support our initial hypothesis of increased gene flow in migratory birds compared to sedentary birds: population subdivision is significantly shallower in migratory birds compared to sedentary birds. A second prediction from our hypothesis is that in both migratory and sedentary birds, gene flow would decline with increasing distance between populations, reducing the degree of similarity in allelic composition; we expected that this decline in gene flow with increasing distance would be more pronounced in the sedentary compared to the migratory birds. We found the predicted distance effects in the sedentary populations, as the number of immigrants per generation declined significantly with increasing distance between populations. Contrary to our expectations, distances up to 350 km between breeding populations did not affect gene flow in the migratory House Wrens, and the allelic composition of the populations was not different at distances between 25 and 350 km.

Recent data from Yellow Warblers (*Dendroica petechia*), which also are long distance migrants, indicate that there is a large-scale geographical pattern in genetic similarity among populations (Gibbs et al. 1997); this pattern divides the North American continent in two population sections, or lineages, east and west of the Great Lakes, and suggests isolation by distance. On the other hand, these results on Yellow Warblers also indicate that movements are common between nesting localities within a large geographic range, a fact that agrees with our observations of high genetic similarity among populations of migratory House Wrens within our 350-km long sampling area in Ohio. Gibbs et al.'s (1997) information on Yellow Warblers and our own on House Wrens support Rockwell and Barrowclough's (1987) estimation of high gene flow in migratory birds.

In the initial design of this project, a within-taxon/across-latitude comparison was chosen over a within-latitude/across-taxa comparison. For example, we could have compared the genetic structure of year-round residents in Ohio (e.g., cardinals, chickadees, woodpeckers) with that of latitudinal migrants breeding in the same place. We chose the within-taxon comparison to avoid possible effects resulting from species differences in evolutionary history that might obscure a relationship between migratory behavior and gene flow. Such within-taxon comparisons are recognized by Bohonak (1999) as being particularly useful in determining the relationship between dispersal and gene flow, which may be

obscured by historical events (Boileau et al. 1992, Pogson et al. 1995). In comparisons between species that are phylogenetically and ecologically similar, those with life history or habitat characteristics that indicate reduced dispersal should show a higher value of F_{ST} and a larger number of private alleles, which should be negatively correlated with dispersal and gene flow (Colgan and Ponder 1994). Our results for these measures of gene flow agree with the expectations of reduced dispersal in sedentary House Wrens compared to migratory House Wrens. We do not know the significance of the skewed distribution of private alleles toward peripheral populations among both migratory and sedentary populations of House Wrens. We speculate that such a result could be due to undetected natural discontinuities in the birds' distributions, or an artifact produced by our sampling scheme (following Colgan and Ponder 1994).

Our present approach allows us to consider other factors affecting the degree of gene flow and population subdivision in both migratory and sedentary birds. A separate data set in which we analyzed population structure in migratory and sedentary Grasshopper Sparrows *Ammodramus savannarum* (Arguedas et al., unpubl. data), suggests that the characteristics of the optimal breeding habitat may also affect the patterns of gene flow among populations. Temporally or spatially unstable habitats would be occupied by species with high dispersal tendencies, as this trait would facilitate the search for such ephemeral, optimal habitat. This relationship between habitat stability and dispersal has been analyzed by McPeek and Holt (1992) and more recently by Paradis (1998). In their models, higher dispersal ability should be maintained in organisms inhabiting spatially and temporally unstable environments. The loss of dispersal ability should be more pronounced in organisms preferring spatially more continuous environments, or environments that are temporally more stable. The habitat of the sedentary House Wren is not only relatively stable, but it also is common and widespread (Skutch 1960, Stiles and Skutch 1989). Sedentary House Wrens would not need to move long distances to find appropriate habitat. In the event of local disturbance to a patch of breeding habitat, adequate replacement habitat is usually found nearby. This results in reduced dispersal as distance between populations increases. During the breeding season, the hab-

itat of migratory House Wrens is just as common and widespread as that of the sedentary birds (Bent 1964). For this reason, habitat characteristics could not account for the high levels of gene flow observed in the migratory birds.

High levels of gene flow might also be characteristic of other migratory species. Most migratory passerines start their southbound movement soon after fledging, often in a wandering, random path that allows the temporary occupation of different sites throughout the season. If site fixation occurs, it might occur at any of those sites, compelling the birds to nest in areas different from their natal site. But even if fixation does not occur, this post-fledging dispersal behavior may familiarize the birds with several sites, from which they might be able to choose for breeding as they return from their wintering grounds (Gauthreaux 1980). Such pre-migratory dispersal behavior, together with low levels of natal or breeding philopatry, would result in extensive mixing of populations. As our observations indicate, erosion of genetic diversity due to population isolation should not be a cause for concern in migratory House Wrens. This may also be the case for other migratory passerines that breed in temporally and spatially stable habitats.

ACKNOWLEDGMENTS

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