The Wilson Journal of Ornithology 118(2):194–207, 2006

MORPHOLOGICAL VARIATION AND GENETIC STRUCTURE OF GALAPAGOS DOVE (*ZENAIDA GALAPAGOENSIS*) POPULATIONS: ISSUES IN CONSERVATION FOR THE GALAPAGOS BIRD FAUNA

DIEGO SANTIAGO-ALARCON,[1,3] SUSAN M. TANKSLEY,[2] AND PATRICIA G. PARKER[1]

ABSTRACT.—Island species, particularly endemics, tend to have lower genetic diversity than their continental counterparts. The low genetic variability of endemic species and small populations has a direct impact on the evolutionary potential of those organisms to cope with changing environments. We studied the genetic population structure and morphological differentiation among island populations of the Galapagos Dove (*Zenaida galapagoensis*). Doves were sampled from five islands: Santa Fe, Santiago, Genovesa, Española, and Santa Cruz. Five microsatellite markers were used to determine genetic diversity, population structure, gene flow, and effective population sizes. F_{ST} and R_{ST} values did not differ among populations; in general, populations with greater geographical separation were not more genetically distinct than those closer to one another, and estimated gene flow was high. There were no significant differences in allelic richness and gene diversity among populations. Although there was extensive morphological overlap among individuals from different island populations for both males and females, we found significant differences in overall body size only between populations on Santa Fe and Santa Cruz (males and females) and between Española and Santa Fe (males only). Significant differences in body size between populations undergoing high rates of gene flow indicate that differentiation may be due to either phenotypic plasticity or ecotypic differentiation. Based on the results of previously conducted disease surveys, we discuss the conservation implications for the Galapagos Dove and other endemics of the archipelago; we also discuss the possible effects of wind currents on gene flow. *Received 24 January 2005, accepted 28 November 2005.*

Historically, islands are places where the most dramatic morphological and genetic differentiations have occurred (Grant 1998, 2001). Geographic isolation between populations is expected to promote differentiation of both morphological and genetic characters, due to either drift or different selective regimes (Slatkin 1985, Bohonak 1999). This may reflect population divergence due to insufficient gene flow that would counteract the effects of drift and selection (Slatkin 1985, Hutchison and Templeton 1999, Coleman and Abbott 2003). Isolation leads to the formation of geographical races, which is considered one of the initial stages of speciation (Grant 2001). However, factors independent of geographical isolation (e.g., microclimate, resources, habitat structure) may be acting to create differences between sympatric populations or populations undergoing high gene flow (e.g., Schluter 2001, Ogden and Thorpe 2002). There is also the possibility that morphological differences may be observed—either immediately or within a few generations—at different geographic locations (different populations) without corresponding genetic differentiation (phenotypic plasticity; e.g., James 1983, Losos et al. 1997, Trussell and Etter 2001).

Island species have served as models for studies of evolution due to the discrete nature of island archipelagos and the isolation between different island populations of the same species. Several Galapagos archipelago endemics have very limited inter-island movement, resulting in morphological differences (e.g., Bollmer 2000, Grant 2001). Columbiformes on the other hand are strong fliers able to move long distances (Goodwin 1977, Baptista et al. 1997). Because of the proximity of several islands in the archipelago, we expected high gene flow among populations of the Galapagos Dove (*Zenaida galapagoensis*) and no morphological differentiation.

The Galapagos Dove is an endemic species whose biology and ecology are poorly understood. Our knowledge of this species is restricted to taxonomic relationships (Goodwin 1977, Johnson and Clayton 2000), morphological descriptions (Ridgway 1897, Gifford

[1] Dept. of Biology, Univ. of Missouri-St. Louis, 8001 Natural Bridge Rd., St. Louis, MO 63121, USA.
[2] Dept. of Animal Science, Kleberg Center, Texas A&M Univ., College Station, TX 77843-2471, USA.
[3] Corresponding author; e-mail: onca77@yahoo.com

1913, Prestwich 1959), and more recently, to some aspects of its breeding and feeding ecology on Genovesa Island (Grant and Grant 1979). Morphological and ecological studies of bird species in the Galapagos archipelago have been mostly restricted to Darwin's finches (Bowman 1961; Boag 1981, 1983; Grant et al. 1985; Grant 2001), Galapagos mockingbirds (*Nesomimus* spp.; Curry 1988, 1989; Curry and Grant 1989), and the Galapagos Hawk (*Buteo galapagoensis*; de Vries 1973, 1975; Bollmer et al. 2003). Measurements and a general description of Galapagos Doves are provided by Ridgway (1897), Gifford (1913), and Swarth (1931). Gifford (1913) suggested that doves inhabiting the northern-most islands—Wolf (formerly Wenman) and Darwin (formerly Culpepper)—are larger than those located within the main cluster of islands; for this reason, dove populations were classified as two subspecies: *Z. g. exsul* (on Wolf and Darwin) and *Z. g. galapagoensis* (Swarth 1931, Baptista et al. 1997). To assess levels of population structure and morphological variation, our study focused on populations of the southern subspecies (*Z. g. galapagoensis*).

Island species, particularly endemics, tend to have lower genetic diversity than their continental counterparts, especially when such species inhabit small islands (Frankham 1996, 1997). Maintaining genetic diversity and understanding patterns of genetic diversity in natural populations is a central issue in conservation genetics (Frankham 1996, 1997, 1998). Populations are not equivalent in their capacity to adapt to changing environmental conditions, and genetic diversity maximizes the potential evolutionary responses of conserved populations (Petit et al. 1998, Hedrick 2001). Species inhabiting islands are considered behaviorally and physiologically naïve; thus, they might be affected more severely than mainland species by the introduction of predators and diseases (Mack et al. 2000). Demographic and environmental stochasticity can be accentuated in small island populations with little genetic variability, increasing their risk of extinction (Frankham 1996, 1997, 1998).

The introduction of exotic organisms to islands is one of the most important factors in the extinction of endemic species (Wikelski et al. 2004). Because of the negative impact of pathogens on the avian endemics in several other archipelagos, preventing the introduction of avian diseases is a conservation priority in the Galapagos archipelago (Padilla et al. 2004, Wikelski et al. 2004). Some diseases common to Columbiformes, such as *Trichomonas gallinae*, might be transmitted to Galapagos Doves by other Columbiformes, such as the exotic Rock Pigeon (*Columba livia*) and the transient (from South America) Eared Dove (*Z. auriculata*; Harmon et al. 1987, Curry and Stoleson 1988, McQuistion 1991, Mete et al. 2001, Padilla et al. 2004). Padilla et al. (2004) have reported a >85% prevalence of *Haemoproteus* malaria in Galapagos Doves and infections of *Chlamydophila psittaci* in doves inhabiting the island of Española. Buckee et al. (2004) have shown theoretically that host spatial structure directly affects pathogen diversity and strain structure. Thus, it is a conservation priority to understand the movement patterns of those species that could serve as vectors or reservoirs of diseases with interspecific infection potential. We have shown how lice from Galapagos Doves can be transmitted to Galapagos Hawks when they prey on doves; predation may represent a route of transmission for several infectious agents transmitted by lice (Whiteman et al. 2004).

Among the islands sampled in this study, only Santa Cruz was inhabited by humans, and it holds the largest human population of the inhabited islands in the archipelago. Española was the most isolated island, lying at the southeastern extreme of the archipelago. Santa Fe and Genovesa were the smallest islands, and Genovesa was the northern-most island (Fig. 1). The Galapagos islands selected for this study—Santiago, Santa Cruz, Santa Fe, Genovesa, and Española—were chosen to represent the maximum geographic isolation between populations (e.g., Española versus Genovesa) and widest (east-west and north-south) coverage of the archipelago that our budget and logistical restrictions could accommodate. In this study, we (1) used principal components analysis (PCA) to examine morphological variation, (2) used five microsatellite loci to describe the population structure and genetic diversity, and (3) estimated effective population sizes and gene flow of *Z. galapagoensis* on five islands of the Galapagos archipelago: Santiago, Santa Cruz, Santa Fe,

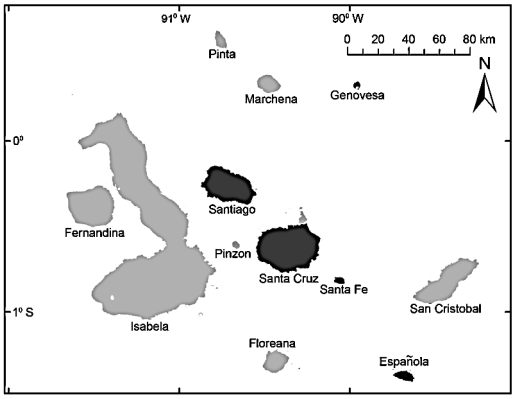

FIG. 1. Map of the Galapagos archipelago, Ecuador, showing the five islands (in dark gray) where Galapagos Doves were sampled in 2002 and 2004. The Galapagos Dove occurs on all the major islands of the archipelago.

Genovesa, and Española. Specifically, we asked (1) are there significant morphological differences among island populations of the Galapagos Dove, (2) are these populations isolated, and (3) is there evidence of low genetic variability in the Galapagos Dove?

METHODS

Field methods.—We conducted our study in the Galapagos archipelago from May through July 2002 and from June through July 2004. Following the guidelines described in Ralph et al. (1996), we captured Galapagos Doves by using hand nets and mist nets. We took blood samples (50 μl each) by venipuncture of the brachial vein from 25 birds each on Santa Cruz, Santa Fe, and Española, and 30 birds each on Santiago and Genovesa islands (Fig. 1). Samples were mixed 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). We also measured 25 birds each from Santa Cruz, Santa Fe, and Española islands and 30 each from Santiago and Genovesa islands (Fig. 1). During the 2002 study season, we sampled doves on San Cristóbal Island, but due to the small sample size (n = 2) they were not included in our analysis. Endemics on San Cristóbal are rare, and the Galapagos Dove seems to be among the rarest.

In order to quantify inter-population differences in morphology, we took the following measurements to the nearest 0.1 mm from the right side of each individual: (1) tarsus length, (2) tail length, (3) length of exposed culmen (from terminus of the feathering to the bill's tip), (4) bill width (calipers were oriented at a 90° angle to the axis of the bill and measurement was taken at the terminus of the feathering), and (5) bill depth (at the terminus of the feathering and again at a 90° angle to the axis of the bill). Using a ruler with a brass perpendicular stop, we also measured wing chord length (unflattened, from carpal joint to the tip of the longest primary) to the nearest 0.5 mm. We used Pesola scales (100 and 300 g) to measure mass to the nearest 0.1 g. Bird measurements were taken by DSA on all the islands but Santa Fe, where J. L. Bollmer conducted the sampling.

Using plumage patterns, we identified birds as adults or juveniles: adults have brighter coloration, and juveniles are much duller in color (Ridgway 1897). Because individual adults of some dove species do not have completely ossified skulls (Pyle 1997), and because the use of cranium calcification (pneumatization) for aging doves is not well developed (Pyle 1997), any captured individual with incomplete calcification and adult coloration was considered an adult. Although it is possible to identify males and females in the field by their plumage coloration and body size (males and females have similar coloration patterns, but males tend to be brighter than females and are larger; Ridgway 1897, Gifford 1913; DSA and PGP unpubl. data), this technique is not always reliable due to individual variation. Therefore, we used a polymerase chain reaction- (PCR) based technique for sexing every individual (Fridolfsson and Ellegren 1999). Birds were released within 40 m of capture location.

Morphology

Statistical analyses.—We used Principal Component Analysis (PCA) to describe morphological variation among islands (SPSS, Inc. 2001). Prior to PCA, variables were checked for outliers (standardizing to zero mean and unit variance); four values with standard deviations ≥2.5 were eliminated. Although all variables (raw data) were normally distributed (Kolmogorov-Smirnov test, $P \geq 0.06$) and have the same scale and dimension (except mass), they were log-transformed in

TABLE 1. Microsatellite primers and number of alleles scored for Galapagos Doves from five islands sampled in 2002 and 2004, Galapagos Islands, Ecuador (n = 134).

Locus	Primer sequence 5′–3′	T_A[a]	No. alleles
WU7a117F	CTC AGT GTA AAT ATG GCA GGG AAT C	54	7
WU7a117R	CAG GTC TTT TTG GTG GAT GTC AC		
WUa38F	GGA GGG CAC CAG AGT TG	55	7
WUa38R	GAT AAG ACC CGA CTT TCA GC		
WUe1F	CAG TGT GGC AGG TAC TTC A	54	3
WUe1R	CTC ATT AGT GGA CCT TGG AC		
WUj22F	CAG GAG CCA TCG TAC ACA T	56	5
WUj22R	TGA ATT ACC CCA TCA ACA AG		
CliμT17	See Traxler et al. 2000	55	11

[a] Annealing temperature (°C).

order to examine proportional contributions of large and small measurements equally. We used PCA on the correlation matrix because one of the variables (mass) did not have the same dimension, and because a PCA on a correlation matrix applied to transformed data is equivalent to a variance-covariance matrix analysis (McGarigal et al. 2000). Furthermore, a PCA from a variance-covariance matrix applied to untransformed (raw) data will give more weight to variables with large variance, which will have a larger influence on the PCA (McGarigal et al. 2000). Because males are larger than females, analyses describing the morphological variation among islands were conducted separately for each sex to prevent the variance due to sexual dimorphism from masking variation among populations. For each PCA, principal component scores were normally distributed (Kolmogorov-Smirnov test, $P \geq 0.74$). Communalities (total variation extracted from each variable) are reported for each PCA. All components with eigenvalues ≥ 1 were retained for subsequent analyses. Eigenvectors were rotated using varimax rotation and retained when the explained variance was higher than that of unrotated components or when the interpretation of PCs was easier. After conducting a PCA for females, we did not find significant differences between adult and juvenile females ($t_{46} = -0.69$, $P = 0.48$); thus, we retained both groups in the PCA. However, we did find significant differences between adult and juvenile males ($t_{67} = 4.23$, $P < 0.001$) and removed juveniles (15) from the male pool. We excluded female bill depth from the analyses for inter-island comparisons because only one such record was available for Santiago Island. We used *t*-tests and ANOVAs on PC scores for group comparisons and Tukey post-hoc tests any time an ANOVA was significant. In every case, variances of PC scores were homogeneous between and among groups (Levene's test, $P > 0.25$). All *t*-tests were independent and two-tailed.

Genetics

DNA isolation and amplification.—DNA extractions by phenol-chloroform were followed by dialysis in 1× TNE_2 (10 mM Tris-HCl, 10 mM NaCl, 2 mM EDTA) and diluted to a working concentration of 20 ng/μl. Integrity and concentration of each DNA sample was determined by spectrophotometry and electrophoresis in 0.8% agarose gels run in 1× TBE. Individuals were scored at four polymorphic microsatellite loci (Table 1) originally developed for White-winged Doves (*Z. asiatica*; accession numbers for WU7a117, WUe1, WUa38, and WUj22 are AF260574, AF260573, AY428751, and AY428752, respectively) and one locus developed for Rock Pigeon (Traxler et al. 2000). We prepared PCR reactions of 10 μl that included 50 ng of whole genomic DNA, 1 mM dNTP's, 10× reaction buffer, 25 mM $MgCl_2$, 0.5 μg of each primer, 0.1 μl of DMSO, and 0.5 units of *Taq* DNA polymerase (SIGMA). PCR conditions were as follows: initial denaturation at 94° C for 3 min followed by 35 cycles of denaturation at 94° C for 30 sec; annealing from 54 to 56° C (see Table 1) for 1 min and extension at 72 C for 1 min; and a final extension at 72° C for 10 min. PCR products were separated in non-denaturing 7.5% polyacrylamide gels run on BioRad sequencing rigs. Gels were

TABLE 2. Principal component (PC) scores and communalities for seven morphological variables of male (n = 50) and female (n = 52) Galapagos Doves sampled from five islands in 2002 and 2004, Galapagos Islands, Ecuador. PC scores represent the correlations of each variable with the principal components; communalities represent the sums of squares of correlation coefficients on the first two PCs or the proportion of variance extracted from each variable.

	Males			Females		
Variable	PC1	PC2	Communalities	PC1	PC2	Communalities
Culmen	0.626	−0.212	0.508	0.614	0.515	0.678
Bill width	0.331	0.734	0.762	0.172	0.639	0.918
Bill depth	0.492	0.272	0.550	—[a]	—	—
Tarsus	0.367	0.644	0.888	0.720	0.331	0.629
Tail	0.786	−0.101	0.692	0.421	−0.642	0.820
Wing	0.674	−0.256	0.604	0.790	−0.006	0.739
Weight	0.779	−0.294	0.696	0.606	−0.644	0.787

[a] Not included.

stained with 0.05% ethidium bromide (EtBr) and visualized using a Kodak UV digital imager (KODAK image station 440CF).

Statistical analyses.—We calculated genetic diversity using Nei's unbiased estimator (Nei 1973), which is the probability that two alleles randomly sampled from a population are different. We analyzed allelic richness through rarefaction analysis as implemented by El Mousadik and Petit (1996) and Petit et al. (1998).

F_{ST} estimates outperform R_{ST} counterparts under some circumstances (e.g., when there are allele size constraints in a microsatellite marker, size differences cannot be used to reflect distances among alleles), even under the stepwise mutation model (SMM). Furthermore, R_{ST} can be less accurate at reflecting population differentiation due to its greater associated variance. Even a small number of random mutation events tends to erase part of the memory of the mutation process that is the base of the SMM, which makes R_{ST} estimates superior to F_{ST} only when the mutation process follows the SMM exactly (Gaggiotti et al. 1999, Balloux et al. 2000, Balloux and Lugon-Moulin 2002). Due to the uncertainty of the mutation process of microsatellites (Primmer and Ellegren 1998, Goldstein and Schlötterer 1999), we decided to use *F*-statistics (Weir and Cockerham 1984) for our analysis. For the sake of comparison, we also calculated R_{ST} across samples, and the significance of population differentiation based on F_{ST} was evaluated using a *G*-test and 1,000 randomizations (Goudet et al. 1996). We used pairwise F_{ST} values and geographic distance matrices to test for isolation by distance (Slatkin 1993, Hutchison and Templeton 1999); significance was evaluated with a Mantel test (Mantel 1967) and distance was log-transformed before analysis. Geographical distance was measured as the closest distance between islands.

Data were analyzed for linkage disequilibrium and Hardy-Weinberg equilibrium using F_{IS}, and testing was conducted via *G*-test and randomization procedures (Goudet et al. 1996, Goudet 1999). Bonferroni corrections were applied when appropriate (Rice 1989). Loci proved to be in linkage equilibrium after 200 permutations ($P \geq 0.08$, Bonferroni corrected *P*-value at $\alpha = 0.05$ was 0.005). Samples were under Hardy-Weinberg equilibrium after 500 randomizations, except for one locus/population (WU7a117, $P = 0.002$ for Santiago Island, Bonferroni corrected *P*-value at $\alpha = 0.05$ was 0.002). Therefore, we tested for population differentiation without assuming *H-W* equilibrium. Analyses were conducted using FSTAT (Goudet 2002).

Because gene flow and effective population size estimates based on F_{ST} depend on many unrealistic assumptions (Waples 1998, Whitlock and McCauley 1999), we used a coalescent-based approach to calculate migration rates (Nm) and theta ($\theta = 4Ne\mu$, which is a genetic diversity parameter related to the effective population size [Ne] from which Ne can be estimated) using the program MIGRATE (Beerli and Felsenstein 1999, 2001). Unlike F_{ST}, this program accounts for directional gene flow and for differences in popu-

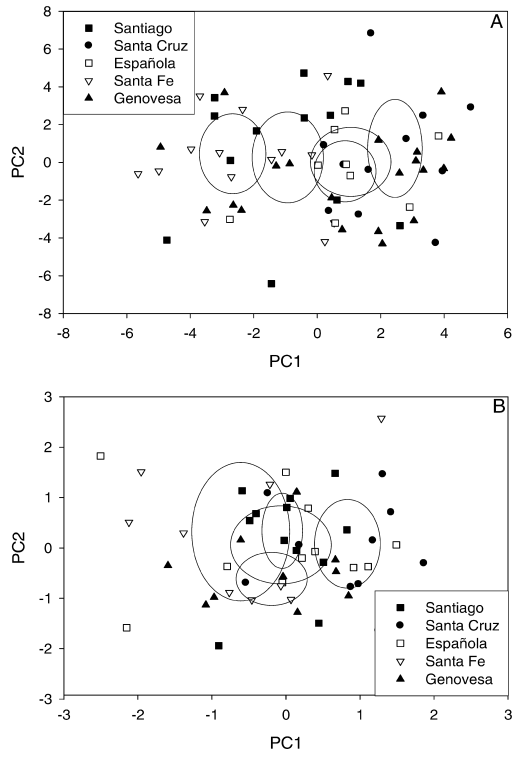

FIG. 2. (A) Morphological ordination space between islands for adult male Galapagos Doves. PC1 is an axis of overall body size and PC2 is a vector reflecting bill size and tarsus length (n = 50). Sample sizes per island were as follows: Santiago (18), Santa Cruz (15), Española (11), Santa Fe (15), and Genovesa (20). (B) Morphological ordination space between islands for female Galapagos Doves. PC1 is an axis of overall body size and PC2 is a vector reflecting bill size and tarsus length (n = 52). Sample sizes per island were as follows: Santiago (12), Santa Cruz (10), Española (14), Santa Fe (10), and Genovesa (10). Ellipses represent the 95% confidence interval for the different islands.

lation size. We ran the program five times using the estimates of each run as starting parameters for the next one. We assumed equal mutation rates among loci, which is an unrealistic assumption (Goldstein and Schlötterer 1999); however, it provides better estimates of parameters than when using variable mutation rates among loci, which increase the variance (Beerli and Felsenstein 1999). We estimated parameters for the first run, since using an F_{ST} initial estimate produced an attraction to the area of the likelihood surface of the generated F_{ST} values, thus preventing the program from searching efficiently throughout the likelihood surface (P. Beerli pers. comm.). Ten short chains and two long chains were used to calculate parameters. We sampled 500 genealogies for each short chain and 5,000 for each long chain; increments were set to 20 for the short chains and to 100 for the long chains; an initial stabilizing period (burn-in) was set to 10,000 genealogies. We computed multiple estimation of parameters using the two long chains of each run. Because MIGRATE calculates historical migration rates, we used the assignment/exclusion method of Cornuet et al. (1999), implemented in the program GENECLASS (Piry et al. 2004), to estimate current levels of gene flow. This method is appropriate to use when all possible sources of migrants (populations) have not been sampled (Cornuet et al. 1999, Berry et al. 2004). We used the ''leave one out'' criterion, which removes the individual for which probabilities of assignment/exclusion to a specific population are calculated (Berry et al. 2004). We used the simulation algorithm of Paetkau et al. (2004) to estimate assignment/exclusion probabilities (α = 0.05, 10,000 simulated individuals).

RESULTS

Morphological variation of males among islands.—We retained the first two principal components. PC1, representing an overall size dimension, explained 36% of the variance. PC2, a bill- (width and depth) and tarsus-length component, explained 17% of the variance. The variance extracted from each variable was >50% (Table 2). There were significant differences among islands in the doves' overall body size (PC1, $F_{4,45}$ = 4.99, P = 0.002; Fig. 2a), but not bill size (PC2, $F_{4,45}$ = 1.53, P = 0.21). Based on PC1, Santa Cruz and Española doves were significantly larger than Santa Fe doves (Tukey-test, *HSD* = 1.16, P = 0.033 and *HSD* = 1.23, P = 0.019, respectively). There is overlap, however, among individuals of these three islands, as well as those from the other islands (Fig. 2a).

Morphological variation of females among islands.—We retained the first two principal components. PC1, which represents an overall size dimension, explained 37% of the variance (Table 2). PC2, a bill- (culmen length and

TABLE 3. Genetic diversity (Nei 1973) and allelic richness for Galapagos Dove, as estimated by rarefaction analysis (Petit et al. 1998) per locus and population. Samples were collected from five islands in 2002 and 2004, Galapagos Islands, Ecuador.

	Genetic diversity				
Locus	SF[b]	E	SC	S	G
Wu7a117	0.75	0.73	0.66	0.69	0.72
Wua38	0.56	0.71	0.52	0.55	0.67
Wue1	0.35	0.42	0.24	0.24	0.31
Wuj22	0.49	0.55	0.62	0.56	0.61
CliμT17	0.79	0.84	0.78	0.84	0.79
Mean ± SD	0.59 ± 0.18	0.65 ± 0.16	0.56 ± 0.20	0.58 ± 0.22	0.62 ± 0.18

[a] R_T = estimated allelic richness for all islands.
[b] SF = Santa Fe, E = Española, SC = Santa Cruz, S = Santiago, G = Genovesa.

width) and tarsus-length component, explained 23% of the variance. The variance extracted from each variable was >62% (Table 2). There were significant differences among islands in overall body size (PC1, $F_{4,47} = 3.14$, $P = 0.023$; Fig. 2b), but not in the second component (PC2, $F_{4,47} = 0.84$, $P = 0.51$). Differences in overall body size were found only among doves from Santa Cruz and Santa Fe, where Santa Cruz females were larger than those from Santa Fe (Tukey-test, $HSD = 1.53$, $P = 0.005$); otherwise there was extensive overlap among individuals from the different islands (Fig. 2b).

Population structure and genetic diversity.—We scored 33 alleles for five polymorphic microsatellite loci from 25 doves on Santa Cruz, Santa Fe, and Española, 30 on Santiago, and 29 on Genovesa. Santa Fe doves had the fewest alleles (23); Española and Santiago had 29 each, Genovesa had 25, and Santa Cruz had 26. The populations with the richest allelic composition (Santiago and Española) had 86% ([29 − 5]/[33 − 5]) of the allelic diversity (excluding the five alleles that were automatically present because there are five loci). Rarefaction analysis showed the same tendency in allelic richness among populations; allelic richness across loci and samples was 27 (Table 3). Genetic diversity was greatest among doves from Española and lowest among those from Santa Cruz; however, there were no significant differences among islands for either allelic richness or genetic diversity (both $P > 0.19$).

Estimates of F_{ST} (0.01, $P > 0.43$) and R_{ST} (0.0057, $P > 0.43$) across samples showed no genetic structure. The 95% bootstrap confidence intervals of the overall F_{ST} estimate were −0.001 and 0.02. No pairwise F_{ST} values were significantly different (all $P \geq 0.025$, Bonferroni corrected P-value at $\alpha = 0.05$ was 0.005; Table 4), and we failed to detect isolation by distance in our data set (Mantel test after 2,000 randomizations, $P > 0.25$).

We estimated high levels of historical gene flow between populations of the Galapagos Dove (Table 5). The highest estimated number of migrants per generation was 71 (Española to Genovesa), which was surprising considering that they are separated by the largest geographic distance (~200 km) compared with distances between the other islands sampled. Genovesa Island had the highest theta value (1.91) and Santa Fe had the lowest (0.18). The high theta for Genovesa is surprising because it is the smallest island of those included in the study; however, Santa Cruz, the largest island, had the second lowest theta value (0.4). If we assume that microsatellite markers have a mutation rate of 10^{-4} events per locus per generation (Goldstein and Schlötterer 1999), and that this mutation rate is the same for each locus, the effective population sizes are as follows: Santa Fe 463; Española 3,600; Santa Cruz 1,000; Santiago 4,600; and Genovesa 4,775. The current high rate of gene flow, as estimated with GENECLASS, suggests that doves are moving among islands. The assignment analysis correctly allocated 27.6% (37) of the individuals ($P \leq 0.009$), but most (34 of 37) had likelihoods lower than the threshold value of being assigned to another population. The difficulties of assigning individuals suggest high current gene flow among populations. Analyses

TABLE 3. Extended.

Allelic richness					
SF	E	SC	S	G	R_T[a]
5	7	6	6.75	4.98	6.11
6	6	5	3.97	4.96	5.46
2	3	2	2.99	2.00	2.56
4	4	4	4.97	4.98	4.61
6	9	9	9.63	7.70	8.25
4.6 ± 1.67	5.8 ± 2.38	5.2 ± 2.58	5.8 ± 2.77	5.0 ± 2.12	5.4 ± 2.08

to detect first generation (F_0) migrants detected 15 migrants ($P \leq 0.05$; Table 6).

DISCUSSION

In this study, we present evidence that populations of Galapagos Doves are morphologically and genetically similar, which must be, in part, the result of high rates of gene flow among islands. However, our results also indicate that there are morphological differences between doves from some island pairs. This might be due to different abiotic and biotic pressures operating on different islands (see below) and to the degree of connectedness (gene flow) between some island pairs (Table 5). For example, Santa Cruz and Santa Fe doves differ in body size (both males and females) and gene flow estimates for these islands are low (see Table 5) even though they are the closest among all the island pairs (17.5 km). Genovesa, the island with the largest effective population size, is the smallest island of those sampled and is also the one receiving the largest number of migrants from the other islands. In addition, it is remarkable that the lowest F_{ST} value and highest numbers of migrants coming to Genovesa are from Española, which is the island most distant from Genovesa (Fig. 1, Tables 4 and 5). Dove populations on both Genovesa and Española, which are small and relatively isolated compared with the central islands (Fig. 1), are the two populations with the greatest genetic diversities, largest estimated population sizes, and highest rates of gene flow (Tables 3 and 5).

Environmental factors such as wind currents might be influencing the travel routes selected by doves from different islands, thus affecting the degree of connectivity among island populations. Several phylogeographic reconstructions of other vertebrate endemics of the archipelago have shown that present and historical wind and ocean currents have had a south-southeast to north-northeast effect on the evolutionary history of organisms (e.g., Caccone et al. 1999, 2002; B. S. Arbogast unpubl. data). However, it is difficult to believe that wind currents are the main reason for movements of Galapagos Doves among islands. Even though there is a high rate of gene flow in a south-to-north direction (e.g., Española to Genovesa [71.4], Española to Santa Cruz [17.85]), gene flow is also high in the

TABLE 4. Estimates of genetic differentiation for Galapagos Doves sampled from five islands in 2002 and 2004, Galapagos Islands, Ecuador. Pairwise F_{ST} values are above, and *P*-values are below, the dashes (geographic distances in km are given in parentheses). No values were significant (Bonferroni corrected *P*-value at $\alpha = 0.05$ was 0.002).

Island	Santa Fe	Española	Santa Cruz	Santiago	Genovesa
Santa Fe	—	0.0028	0.0033	−0.0036	0.0090
Española	0.22 (74)	—	0.0264	0.0159	−0.0003
Santa Cruz	0.42 (18)	0.16 (99)	—	−0.0096	0.0372
Santiago	0.10 (76)	0.34 (161)	0.66 (24)	—	0.0160
Genovesa	0.035 (135)	0.20 (204)	0.025 (103)	0.095 (100)	—

TABLE 5. Bi-directional gene flow estimates and theta values (95% CI), estimated with MIGRATE (Beerli and Felsenstein 1999, 2001), for Galapagos Doves from five islands, 2002 and 2004, Galapagos Islands, Ecuador.

Island	Theta ($\theta = 4N_e\mu$)	Nm				
		Santa Fe	Española	Santa Cruz	Santiago	Genovesa
1: Santa Fe	0.18 (0.16–0.20)	1 to x[a]	2 to x	3 to x	4 to x	5 to x
2: Española	1.44 (1.31–1.59)	—	4.64 (4.07–5.26)	4.42 (3.86–5.02)	3.91 (3.31–4.48)	6.75 (6.06–7.50)
3: Santa Cruz	0.41 (0.37–0.44)	29.24 (27.20–31.38)	—	36.97 (34.67–39.37)	1.32 (0.92–1.82)	14.12 (12.72–15.63)
4: Santiago	1.84 (1.67–2.03)	0.35 (0.19–0.56)	17.85 (16.58–19.18)	—	10.68 (9.70–11.72)	6.39 (5.64–7.20)
5: Genovesa	1.91 (1.67–2.21)	6.06 (5.07–7.17)	9.59 (8.34–10.97)	5.66 (4.71–6.73)	—	21.52 (19.61–23.55)
		16.13 (14.11–18.33)	71.47 (67.11–76.00)	13.88 (12.01–15.93)	16.54 (14.49–18.77)	—

[a] The population receiving migrants = x, and the number preceding x is the population from where migrants come. For example, in row 1: Population 2 (Española) provides 4.64 migrants per generation to Population 1 (Santa Fe); Population 3 (Santa Cruz) provides 4.42 migrants; Population 4 (Santiago) provides 3.9 migrants; and Population 5 (Genovesa) provides 6.75 migrants per generation to Population 1.

opposite direction (e.g., Santa Cruz to Española [36.9], Santa Fe to Española [29.2], Genovesa to Santiago [21.5], Genovesa to Española [14.2]; Table 5). Hence, wind currents might not completely account for movements among islands. Perhaps the lack of any clear pattern in dove movement among islands is due to the strong flight capabilities of Columbiformes and the short distances between some islands (<20 km). Doves may simply move between islands to track food resources and suitable environmental conditions. The lack of any pattern in isolation by distance among populations supports the idea that doves can move in any direction.

Low genetic differentiation among dove populations might also be accounted for either by a recent population expansion or by the presence of alleles shared due to common ancestry (e.g., Grant et al. 2005), rather than by frequent dispersal between populations. Rapid population expansion could explain reduced within-population diversity (versus global diversity linked to founder events; Hedrick 2000, McCoy et al. 2003). In our study, estimates of genetic diversity were similar among populations, which would support a gene flow explanation instead of a recent expansion. The possible effect of shared alleles due to common ancestry might be ruled out by the results obtained with GENECLASS, which estimated that current rates of gene flow are high. Moreover, if the Galapagos Dove colonized the archipelago between 2.5 and 3 mya, as proposed by Johnson and Clayton (2000), we should have detected a genetic signature of divergence, given isolation (by distance) between populations.

Morphological variation among islands.—Altitudinal and latitudinal patterns of morphological variation within islands have been confirmed for Darwin's finches, but some patterns are not consistent among islands (Grant et al. 1985). For a given finch species, individuals are larger at higher elevations within any one island, but size variation among island populations is not systematically related to either latitude or longitude. However, this is not the case for other endemic species of the archipelago, such as Galapagos Hawks, where there is a clear north- (smaller size) to-south (larger size) trend in morphological variation (Bollmer et al. 2003). Body size variation in

TABLE 6. Gene flow estimates of first generation migrants (F_0), calculated with GENECLASS (Piry et al. 2004), for Galapagos Doves on five islands, 2002 and 2004, Galapagos Islands, Ecuador. *P*-values are given in parentheses.

	Nm				
Island	Santa Fe	Española	Santa Cruz	Santiago	Geneovesa
	1 to x[a]	2 to x	3 to x	4 to x	5 to x
1: Santa Fe	—	1 (0.039)	1 (0.028)	0	0
2: Española	1 (0.025)	—	1 (0.016)	0	0
3: Santa Cruz	2 (0.027)	1 (0.003)	—	0	1 (0.002)
4: Santiago	1 (0.026)	0	2 (0.026)	—	1 (0.004)
5: Genovesa	0	1 (0.006)	1 (0.035)	1 (0.012)	—

[a] The population receiving migrants = x, and the number preceding x is the population from where migrants come. For example, in row 1: Population 2 (Española) provides 1 migrant per generation to Population 1 (Santa Fe); Population 3 (Santa Cruz) provides 1 migrant; Population 4 (Santiago) provides 0 migrants; and Population 5 (Genovesa) provides 0 migrants per first generation to Population 1.

the Galapagos Dove, however, did not show geographical patterns among the group of islands studied here, most likely because (1) environmental characteristics on the different islands do not vary geographically in a simple manner (Grant et al. 1985), and (2) gene flow for doves among islands is greater than it is for finches or hawks (see below). Moreover, the dove's omnivorous diet (see Grant and Grant 1979) could further impede extensive morphological differentiation between island populations—a situation similar to that of Galapagos mockingbirds (B. S. Arbogast unpubl. data) and Hawaiian thrushes (*Myadestes* spp.; Lovette et al. 2001).

Population structure and conservation.—The lack of population structure and the high levels of gene flow and genetic variation are in stark contrast with results reported for other species in the archipelago, which are characterized by divergence among different island populations and low genetic diversity (e.g., Grant 2001, Bollmer 2000, Bollmer et al. 2003). Allelic richness of the Galapagos Dove for the five microsatellite loci genotyped in this study was similar to the values reported for its continental relatives, White-winged Dove (Tanksley 2000) and Mourning Dove (*Z. macroura*; L. M. Reichart unpubl. data), and in some cases it was greater.

Tanksley (2000) used microsatellite markers and reported no genetic structure in White-winged Doves sampled at a broader geographic scale in North America; mtDNA revealed slight differentiation between populations according to a historical east-west division of its distribution (Pecos River in Texas) that is currently disappearing due to the species' range expansion (Pruett et al. 2000). Pruett et al. (2000) suggested that the White-winged Dove's range expansion is due to urban development, which provides water, food, and nesting sites. Urban development also might be affecting Galapagos Dove populations, at least on the two inhabited islands visited in this study (Santa Cruz and San Cristóbal). Santa Cruz doves had the third lowest number of alleles, second lowest effective population size, and the lowest genetic diversity. On San Cristóbal, extensively surveyed for 3 days, we saw and captured only two doves. Population declines of other endemic bird species on San Cristóbal have been reported (Vargas 1996). The rarity of doves and population declines of other endemic bird species on San Cristóbal seem to be due to the large number of introduced species and to the longer history of human settlement (Vargas 1996). These results provide some support for a negative impact of urban development on Galapagos Doves.

Harmon et al. (1987) reported Galapagos Doves infected with *Trichomonas gallinae* (believed to have been transmitted by Rock Pigeons) on Santa Cruz Island, and Padilla et al. (2004) reported infected Rock Pigeons, but no infected Galapagos Doves. Galapagos Doves on Española were infected with *Chlamydophila psittaci*. The prevalence of *Haemoproteus* spp. in Galapagos Doves was found to be >85% on five islands (Padilla et al. 2004). The presence of infectious diseases and mosquitoes of the genus *Culex* (Wikelski et al. 2004, Whiteman et al. 2005)—the vector of some malaria species—poses serious threats to endemic species. The fact that infectious diseases have resulted in epidemics or

epizootics (e.g., *C. psittaci* and *T. gallinae*) in Columbidae and other bird taxa suggests that regular population and disease surveys are needed for Galapagos Doves. High rates of gene flow in Galapagos Doves could contribute to the endangerment of native and endemic species prone to the effects of introduced pathogens that can be transmitted across species (e.g., Galapagos Dove lice being transmitted to Galapagos Hawks during predation; Whiteman et al. 2004). We recommend that the Galapagos Dove be considered a focal species for disease research in the archipelago because it could serve as a reservoir/vector for some infectious diseases (Padilla et al. 2004).

Morphology and dispersal.—That we found morphological differences between some island pairs is not congruent with low genetic differentiation and high rates of gene flow among islands. Lack of concordance between morphology and genetics, however, is not uncommon; through the use of mtDNA markers, it has been reported for other groups, such as reptiles (Schmitt et al. 2000, Brehm et al. 2001), mollusks (Mukaratirwa et al. 1998), insects (Baranyi et al. 1997), and birds (Seutin et al. 1993, 1994; Zink and Dittmann 1993; Freeman-Gallant 1996).

One might expect that morphological differences would have been erased by the connectedness between populations. However, because genes under selective pressure likely control morphological traits, and because F_{ST} assumes neutral markers, selectively neutral markers might not track morphological differences among populations. We do not believe that processes such as genetic drift are important in determining the morphological differences in Galapagos Doves, since they require that gene flow be restricted among populations. Alternatively, morphological characters can be very plastic and might vary within species, depending on the environmental characteristics of an area. Many studies have shown that environmental factors are sufficient to produce morphological changes, either immediately or within a few generations (James 1983, Losos et al. 1997, Trussell and Etter 2001). In other words, environmentally induced differences among populations are independent of genetic differences. Another possibility is that even where dove populations are sympatric and/or affected by high rates of gene flow, there may be an ecotypic-differentiation process driven by divergent selection (Schluter 2001). This has been reported in several studies and for different taxa (Schluter 2001, Ogden and Thorpe 2002). Based on the estimated effective population sizes for the different islands (from ~400 on Santa Fe to ~4,800 on Genovesa), the migration rates (0 to ~70 individuals per generation) represent ~2% of the effective size of the population on the different islands. At this level of migration, the genetic influx might not completely counteract the effects of selection (Conner and Hartl 2004), which could account for the morphological differences observed in our study.

ACKNOWLEDGMENTS

We thank all who provided help during the different stages of the field season, particularly N. K. Whiteman, J. L. Bollmer, G. Jiménez, J. Merkel, J. Rabenold, and N. Gottdenker. We thank the staff of the Charles Darwin Research Station for their invaluable help and logistical support during the course of this study, especially P. Robayo. We also thank N. Freire and J. Miranda who helped with dove sampling at Tortuga Bay, Santa Cruz. Permits for sample collection were provided by Galapagos National Park. We thank B. A. Loiselle, R. E. Ricklefs, B. T. Ryder, A. Cohen, and J. L. Bollmer for helpful comments and suggestions on earlier versions of this manuscript. We thank H. Vargas for sharing his knowledge of Galapagos Doves from islands not visited in this study. We thank P. Beerli who provided guidance on using program MIGRATE. We thank R. L. Curry and two anonymous reviewers for comments that greatly improved the manuscript. Financial support was provided by The International Center for Tropical Ecology, The Saint Louis Zoo, and E. Des Lee Collaborative Vision in Zoological Research.

LITERATURE CITED

BALLOUX, F., H. BRÜNNER, N. LUGON-MOULIN, J. HAUSSER, AND J. GOUDET. 2000. Microsatellites can be misleading: an empirical and simulation study. Evolution 54:1414–1422.

BALLOUX, F. AND N. LUGON-MOULIN. 2002. The estimation of population differentiation with microsatellite markers. Molecular Ecology 11:155–165.

BAPTISTA, L. F., P. W. TRAIL, AND H. M. HORBLIT. 1997. Family Columbidae (pigeons and doves). Pages 60–243 *in* Handbook of the birds of the world, vol. 4: sandgrouse to cuckoos (J. del Hoyo, A. Elliot, and J. Sargatal, Eds.). Lynx Edicions, Barcelona, Spain.

BARANYI, C., G. GOLLMANN, AND M. BOBIN. 1997. Genetic and morphological variability in roach *Ru-*

tilus rutilus, from Austria. Hydrobiologia 350:13–23.

BEERLI, P. AND J. FELSENSTEIN. 1999. Maximum-likelihood estimation of migration rates and effective population numbers in two populations using a coalescent approach. Genetics 152:763–773.

BEERLI, P. AND J. FELSENSTEIN. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in *n* subpopulations by using a coalescent approach. Proceedings of the National Academy of Sciences, USA 98:4563–4568.

BERRY, O., M. D. TOCHER, AND S. D. SARRE. 2004. Can assignment tests measure dispersal? Molecular Ecology 13:551–561.

BOAG, P. T. 1981. Morphological variation in the Darwin's finches (*Geospizinae*) of Daphne Major Island, Galapagos. Ph.D. dissertation, McGill University, Montreal, Canada.

BOAG, P. T. 1983. The heritability of external morphology in Darwin's ground finches (*Geospiza*) on Isla Daphne Major, Galapagos. Evolution 37:877–894.

BOHONAK, A. J. 1999. Dispersal, gene flow, and population structure. Quarterly Review of Biology 74: 21–45.

BOLLMER, J. L. 2000. Genetic and morphologic differentiation among island populations of Galapagos Hawks (*Buteo galapagoensis*). M.Sc. thesis, Ohio State University, Columbus.

BOLLMER, J. L., T. SANCHEZ, M. D. CANNON, D. SANCHEZ, B. CANNON, J. C. BEDNARZ, T. DE VRIES, M. S. STRUVE, AND P. G. PARKER. 2003. Variation in morphology and mating system among island populations of Galapagos Hawks. Condor 105: 428–438.

BOWMAN, R. L. 1961. Morphological differentiation and adaptation in the Galapagos finches. University of California Publications in Zoology, no. 58.

BREHM, A., M. KHADEM, J. JESUS, P. ANDRADE, AND L. VICENTE. 2001. Lack of congruence between morphometric evolution and genetic differentiation suggests a recent dispersal and local habitat adaptation of the Madeiran lizard *Lacerta dugesii*. Genetics Selection and Evolution 33:671–685.

BUCKEE, C. O'. F., K. KOELLE, M. J. MUSTARD, AND S. GUPTA. 2004. The effects of host contact network structure on pathogen diversity and strain structure. Proceedings of the National Academy of Sciences, USA 101:10839–10844.

CACCONE, A., G. GENTILE, J. P. GIBBS, T. H. FRITTS, H. L. SNELL, J. BETTS, AND J. R. POWELL. 2002. Phylogeography and history of giant Galapagos tortoises. Evolution 56:2052–2066.

CACCONE, A., J. P. GIBBS, V. KETMAIER, EL SUATONI, AND J. R. POWELL. 1999. Origin and evolutionary relationships of giant Galapagos tortoises. Proceedings of the National Academy of Sciences, USA 96:13223–13228.

COLEMAN, M. AND R. J. ABBOTT. 2003. Possible causes of morphological variation in an endemic Moroccan groundsel (*Senecio leucanthemifolius* var. *casablancae*): evidence from chloroplast DNA and random amplified polymorphic DNA markers. Molecular Ecology 12:423–434.

CONNER, J. K. AND D. L. HARTL. 2004. A primer of ecological genetics. Sinauer, Sunderland, Massachusetts.

CORNUET, J.-M., S. PIRY, G. LUIKART, A. ESTOUP, AND M. SOLIGNAC. 1999. New methods employing multilocus genotypes to select or exclude populations as origins of individuals. Genetics 153: 1989–2000.

CURRY, R. L. 1988. Group structure, within group conflict and reproductive tactics in cooperatively breeding Galapagos Mockingbirds, *Nesomimus parvulus*. Animal Behaviour 36:1708–1728.

CURRY, R. L. 1989. Geographic variation in social organization of Galapagos Mockingbirds: ecological correlates of group territoriality and cooperative breeding. Behavioral Ecology and Sociobiology 25:147–160.

CURRY, R. L. AND P. R. GRANT. 1989. Demography of the cooperatively breeding Galapagos Mockingbird, *Nesomimus parvulus*, in a climatically variable environment. Journal of Animal Ecology 58: 441–463.

CURRY, R. L. AND S. H. STOLESON. 1988. New bird records from the Galapagos associated with the El Niño-Southern Oscillation. Condor 90:505–507.

DE VRIES, T. J. 1973. The Galapagos Hawk, an ecogeographical study with special reference to its systematic position. Ph.D. thesis, Vrije University, Amsterdam, Holland.

DE VRIES, T. J. 1975. The breeding biology of the Galapagos Hawk, *Buteo galapagoensis*. Le Gerfaut 65:29–57.

EL MOUSADIK, A. AND R. J. PETIT. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic of Morocco. Theoretical and Applied Genetics 92:832–839.

FRANKHAM, R. 1996. Relationship of genetic variation to population size in wildlife. Conservation Biology 10:1500–1508.

FRANKHAM, R. 1997. Do island populations have less genetic variation than mainland populations? Heredity 78:311–327.

FRANKHAM, R. 1998. Inbreeding and extinction: island populations. Conservation Biology 12:665–675.

FREEMAN-GALLANT, C. R. 1996. Microgeographic patterns of genetic and morphological variation in Savannah Sparrows (*Passerculus sandwichensis*). Evolution 50:1631–1637.

FRIDOLFSSON, A. K. AND H. ELLEGREN. 1999. A simple and universal method for molecular sexing of nonratite birds. Journal of Avian Biology 30:116–121.

GAGGIOTTI, O. E., O. LANGE, K. RASSMANN, AND C. GLIDDON. 1999. A comparison of two indirect methods for estimating average levels of gene flow using microsatellite data. Molecular Ecology 8:1513–1520.

GIFFORD, E. W. 1913. Expedition of the California

Academy of Sciences to the Galapagos Islands, 1905–1906. Proceedings of the California Academy of Sciences 2:1–132.

GOLDSTEIN, D. B. AND C. SCHLÖTTERER. 1999. Microsatelites: evolution and applications. Oxford University Press, New York.

GOODWIN, D. 1977. Pigeons and doves of the world. Cornell University Press, Ithaca, New York.

GOUDET, J. 1999. An improved procedure for testing key innovations. American Naturalist 53:549–555.

GOUDET, J. 2002. FSTAT, ver. 2.9.3.2. University of Lausanne, Lausanne, Switzerland. www2.unil.ch/popgen/softwares/fstat.htm (accessed September 2004).

GOUDET, J., M. RAYMOND, T. DEMEEUS, AND F. ROUSSET. 1996. Testing genetic differentiation in diploid populations. Genetics 144:1933–1940.

GRANT, P. R. 1998. Evolution on islands. Oxford University Press, Oxford, United Kingdom.

GRANT, P. R. 2001. Reconstructing the evolution of birds on islands: 100 years of research. Oikos 92: 385–403.

GRANT, P. R., I. ABBOTT, D. SCHLUTER, R. L. CURRY, AND L. K. ABBOTT. 1985. Variation in the size and shape of Darwin's finches. Biological Journal of the Linnean Society 25:1–39.

GRANT, P. R., B. R. GRANT, AND K. PETREN. 2005. Hybridization in the recent past. American Naturalist 166:56–67.

GRANT, P. R. AND K. T. GRANT. 1979. Breeding and feeding ecology of the Galapagos Dove. Condor 81:397–403.

HARMON, W. M., W. A. CLARK, A. C. HAWBECKER, AND M. STAFFORD. 1987. *Trichomonas gallinae* in columbiform birds from the Galapagos Islands. Journal of Wildlife Diseases 23:492–494.

HEDRICK, P. W. 2000. Genetics of populations. Jones and Bartlett, Sudbury, Massachusetts.

HEDRICK, P. W. 2001. Conservation genetics: where are we now? Trends in Ecology and Evolution 16: 629–636.

HUTCHISON, D. W. AND A. R. TEMPLETON. 1999. Correlation of pairwise genetic and geographic distance measures: inferring the relative influences of gene flow and drift on the distribution of genetic variability. Evolution 53:1898–1914.

JAMES, F. C. 1983. Environmental component of morphological differentiation in birds. Science 221: 184–186.

JOHNSON, K. P. AND D. H. CLAYTON. 2000. A molecular phylogeny of the dove genus *Zenaida*: mitochondrial and nuclear DNA sequences. Condor 102: 864–870.

LONGMIRE, J. L., A. K. LEWIS, N. C. BROWN, J. M. BUCKINGHAM, L. M. CLARK, M. D. JONES, L. J. MEINCKE, ET AL. 1988. Isolation and characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. Genomics 2:14–24.

LOSOS, J. B., K. I. WARHEIT, AND T. W. SCHOENER. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 387:70–73.

LOVETTE, I. J., E. BERMINGHAM, AND R. E. RICKLEFS. 2001. Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. Proceedings of the Royal Society of London, Series B 269:37–42.

MACK, R. N., D. SIMBERLOFF, W. M. LONSDALE, H. EVANS, M. CLOUT, AND F. A. BAZZAZ. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10: 689–710.

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

MCCOY, K. D., T. BOULINIER, C. TIRARD, AND Y. MICHALAKIS. 2003. Host-dependent genetic structure of parasite populations: differential dispersal of seabird tick host races. Evolution 57:288–296.

MCGARIGAL, K., S. CUSHMAN, AND S. STAFFORD. 2000. Multivariate statistics for wildlife and ecology research. Springer-Verlag, New York.

MCQUISTION, T. E. 1991. *Eimeria palumbi*, a new coccidian parasite (Apicomplexa: Eimeriidae) from the Galapagos Dove (*Zenaida galapagoensis*). Transactions of the American Microscopical Society 110:178–181.

METE, A., G. H. A. BORST, AND G. M. DORRESTEIN. 2001. Atypical poxvirus lesions in two Galapagos Doves (*Nesopelia g. galapagoensis*). Avian Pathology 30:159–162.

MUKARATIRWA, S., T. K. KRISTENSEN, H. R. SIEGISMUND, AND S. K. CHANDIWANA. 1998. Genetic and morphological variation of populations belonging to the *Bulinus truncatus*/*tropicus* complex (Gastropoda: Planorbidae) in south western Zimbabwe. Journal of Molluscan Studies 64:435–446.

NEI, M. 1973. Analysis of gene diversity in subdivided populations. Proceedings of the National Academy of Sciences, USA 70:3321–3323.

OGDEN, R. AND R. S. THORPE. 2002. Molecular evidence for ecological speciation in tropical habitats. Proceedings of the National Academy of Sciences, USA 99:13612–13615.

PADILLA, L. R., D. SANTIAGO-ALARCON, J. MERKEL, E. MILLER, AND P. G. PARKER. 2004. Survey for *Haemoproteus* spp., *Trichomonas gallinae*, *Chlamydophila psittaci* and *Salmonella* spp. in Galapagos Islands Columbiformes. Journal of Zoo and Wildlife Medicine 35:60–64.

PAETKAU, D., R. SLADE, M. BURDENS, AND A. ESTOUP. 2004. Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. Molecular Ecology 13:55–65.

PETIT, R. J., A. EL MOUSADIK, AND O. PONS. 1998. Identifying populations for conservation on the basis of genetic markers. Conservation Biology 12:844–855.

PIRY, S., A. ALAPETITE, J.-M. CORNUET, D. PAETKAU,

L. BAUDOUIN, AND A. ESTOUP. 2004. GENECLASS2: a software for genetic assignment and first-generation migrant detection. Journal of Heredity 95:536–539.

PRESTWICH, A. A. 1959. The Galapagos Dove in freedom and captivity. Avicultural Magazine 65:66–76.

PRIMMER, C. R. AND H. ELLEGREN. 1998. Patterns of molecular evolution in avian microsatellites. Molecular Biology and Evolution 15:997–1008.

PRUETT, C. L., S. E. HENKE, S. M. TANKSLEY, M. E. SMALL, K. M. HOGAN, AND J. ROBERSON. 2000. Mitochondrial DNA and morphological variation of White-winged Doves in Texas. Condor 102: 871–880.

PYLE, P. 1997. Identification guide to North American birds, part I. Slate Creek Press, Bolinas, California.

RALPH, C. J., G. R. GEUPEL, P. PYLE, T. E. MARTIN, D. F. DESANTE, AND B. MILA. 1996. Manual de métodos de campo para el monitoreo de aves terrestres. General Technical Report 159, USDA Forest Service, Pacific Southwest Research Station, Albany, California.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

RIDGWAY, R. 1897. Birds of the Galapagos archipelago. Proceedings of the U.S. National Museum 19: 459–670.

SCHLUTER, D. 2001. Ecology and the origin of species. Trends in Ecology and Evolution 16:372–380.

SCHMITT, L. H., R. A. HOW, S. HISHEH, J. GOLDBERG, AND I. MARYANTO. 2000. Geographic patterns in genetic and morphological variation in two skink species along the banda arcs, southeastern Indonesia. Journal of Herpetology 34:240–258.

SEUTIN, G. J., J. BRAWN, R. E. RICKLEFS, AND E. BERMINGHAM. 1993. Genetic divergence among populations of a tropical passerine, the Streaked Saltator (*Saltator albicollis*). Auk 110:117–126.

SEUTIN, G. J., N. K. KLEIN, R. E. RICKLEFS, AND E. BERMINGHAM. 1994. Historical biogeography of the Bananaquit (*Coereva flaveola*) in the Caribbean region: a mitochondrial DNA assessment. Evolution 48:1041–1061.

SLATKIN, M. 1985. Gene flow in natural populations. Annual Review of Ecology and Systematics 16: 393–30.

SLATKIN, M. 1993. Isolation by distance in equilibrium and non-equilibrium populations. Evolution 47: 264–279.

SPSS, INC. 2001. SPSS, release 11.0.1. SPSS, Inc., Chicago, Illinois.

SWARTH, H. S. 1931. The avifauna of the Galapagos Islands. Occasional Papers of the California Academy of Sciences, no. 18.

TANKSLEY, S. M. 2000. Analysis of genetic differentiation in White-winged Doves. Ph.D. dissertation, Texas A&M University, College Station.

TRAXLER, B., G. BREM, M. MULLER, AND R. ACHMANN. 2000. Polymorphic DNA microsatellites in the domestic pigeon, *Columba livia* var. *domestica*. Molecular Ecology 9:365–378.

TRUSSELL, G. C. AND R. J. ETTER. 2001. Integrating genetic and environmental forces that shape the evolution of geographic variation in a marine snail. Genetica 112:321–337.

VARGAS, H. 1996. What is happening with the avifauna of San Cristóbal? Noticias de Galapagos 57:23–24.

WAPLES, R. S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. Journal of Heredity 89:438–450.

WEIR, B. S. AND C. C. COCKERHAM. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38:1358–1370.

WHITEMAN, N. K., S. J. GOODMAN, B. J. SINCLAIR, T. WALSH, A. A. CUNNINGHAM, L. D. KRAMER, AND P. G. PARKER. 2005. Detection of the avian disease vector *Culex quinquefasciatus* Say 1823 (Diptera: Culicidae) on the Galapagos Islands, Ecuador, after a 14-year interval. Ibis 147:844–847.

WHITEMAN, N. K., D. SANTIAGO-ALARCON, K. P. JOHNSON, AND P. G. PARKER. 2004. Differences in straggling rates between two genera of dove lice (Insecta: Phthiraptera) reinforce population genetic and cophylogenetic patterns. International Journal for Parasitology 34:113–119.

WHITLOCK, M. C. AND D. E. MCCAULEY. 1999. Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm + 1)$. Heredity 82:117–125.

WIKELSKI, M., J. FOUFOPOULOS, H. VARGAS, AND H. SNELL. 2004. Galapagos birds and diseases: invasive pathogens as threats for island species. Ecology and Society 9(1):5. www.ecologyandsociety.org/vol9/iss1/art5 (accessed 5 January 2005).

ZINK, R. M. AND D. L. DITTMANN. 1993. Gene flow, refugia, and evolution of geographic variation in the Song Sparrow (*Melospiza melodia*). Evolution 47:717–729.