The Condor 108:440–445

ABSENCE OF POPULATION GENETIC STRUCTURE AMONG BREEDING COLONIES OF THE WAVED ALBATROSS

KATHRYN P. HUYVAERT[1] AND PATRICIA G. PARKER
Department of Biology, University of Missouri-St. Louis, MO 63121-4499

Abstract. We used four variable microsatellite loci to examine the distribution of genetic variation and degree of genetic structuring among three subcolonies of Waved Albatrosses (*Phoebastria irrorata*). The breeding population of this species is almost entirely limited to the island of Española in the Galápagos Archipelago. Such strong philopatry could lead to population genetic structure among subcolonies on the island. Pairwise values of the F_{ST} analog, θ, calculated from microsatellite genotypes, were all less than 0.012, indicating little genetic differentiation and the presence of gene flow throughout the population.

Key words: genetic diversity, genetic structure, microsatellite, philopatry, Phoebastria irrorata*, Waved Albatross.*

Ausencia de Estructura Genética entre Colonias Reproductivas de *Phoebastria irrorata*

Resumen. Utilizamos cuatro microsatelites variables para examinar la distribución de la variación genética y el grado de estructura genética entre tres colonias reproductivas de *Phoebastria irrorata*. La población reproductiva entera de esta especie se limita casi totalmente a la isla de Española, en el archipiélago de Galápagos. Un grado de filopatría marcado podría llevar a la formación de estructura genética poblacional entre colonias en la isla. Todos los valores de θ, un análogo de F_{ST}, calculados a partir de genotipos de microsatelites, fueron menores de 0.012, indicando poca diferenciación genética y la presencia de flujo genético a través de la población.

Patterns of behavior such as dispersal and mate choice have important implications for the distribution of genetic variation among and within populations (Chesser 1991, Dieckmann et al. 1999). Gene flow influences ecological associations at multiple scales, such as source-sink relationships among populations in large plant communities (Mouquet et al. 2001) or population- and social group-level genetic differentiation, as in Tanzanian lions (Spong et al. 2002). Reduced dispersal is thought to partly account for lower genetic diversity of island populations relative to their mainland counterparts. In addition, genetic variation of island endemics is typically lower than that of island taxa that have mainland representatives (Frankham 1997). Thus, the strong philopatry of single-island endemics might lead to pronounced genetic differentiation among subpopulations or even social groups on the island.

With the exception of a variable but very small number of individuals on Isla de la Plata (1°16′S, 81°04′W) off the coast of Ecuador, the breeding population of ~19 000 Waved Albatrosses nests exclusively on Española (1°20′S, 89°40′W; Anderson et al. 2003a), the southeasternmost island of the Galápagos Archipelago. Waved Albatrosses are thought to exhibit strong natal philopatry: 93% of 291 birds banded as young from 1963 to 1966 were recaptured as adults "more or less" on their natal nesting sites (Harris 1973:504) and, except for two birds which moved from Punta Suárez on the western tip of Española to Punta Cevallos on the eastern end of the island, the remainder of these young were recaptured within 1 km of the natal site (Harris 1973). The mating system of Waved Albatrosses is characterized by high year-to-year mate and nest-site fidelity (KPH, unpubl. data), also suggestive of high breeding philopatry. This is supported by extensive work by Harris (1973): only 5 of 1273 (0.4%) resighted birds originally marked as adults at known locations were caught at distant sites, at most 2 km from the original banding site; the rest were recaptured at the subcolony where they were banded. Long-term data show similarly high breeding-site fidelity but non-negligible juvenile dispersal rates for a related taxon, the Wandering Albatross (*Diomedea exulans*, Inchausti and Weimerskirch 2002). Given the Waved Albatross population's geographic isolation from the mainland, endemism, and apparent natal- and breeding-site philopatry, we predicted genetic population structure among spatially separated subcolonies on the island of Española. However, even a small degree of natal dispersal may be sufficient to maintain gene flow and genetic homogeneity among subpopulations. Here, we examine these hypothesized relationships between apparent philopatry and the distribution of genetic variation within and among subcolonies of the Waved Albatross using microsatellite genotypes at four loci.

Manuscript received 9 September 2005; accepted 31 January 2006.

[1] Present address: Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523-1474. E-mail: huyvaert@warnercnr.colostate.edu

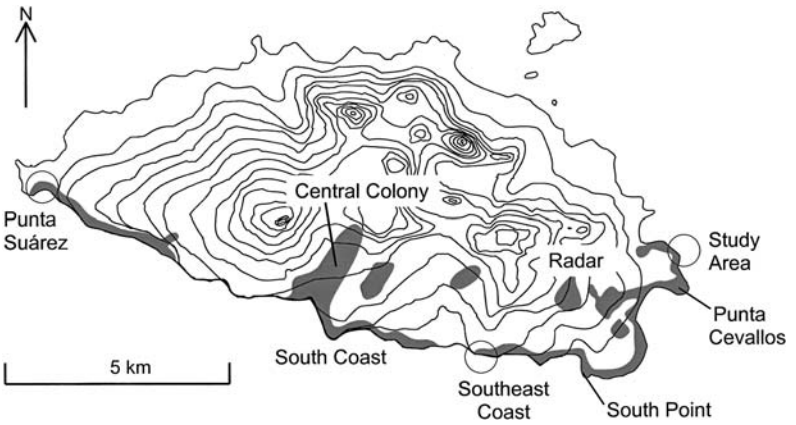

FIGURE 1. Breeding colony locations and genetic variation sampling sites of the Waved Albatross (*Phoebastria irrorata*) on Española, Galápagos, Ecuador (1°20′S, 89°40′W). Shaded areas are breeding colonies identified by Harris (1973). The two small colonies east of the Central Colony have disappeared since Harris's surveys (Douglas 1998, Anderson et al. 2003a). Genetic sampling sites (Punta Suárez, Southeast Coast, and Study Area) are indicated with unfilled circles. Contour lines indicate 15 m changes in elevation. The map is from Harris (1973; Ibis 115:484, fig. 1; reproduced with permission of the Editor).

METHODS

Dense breeding colonies of Waved Albatrosses are situated along the southern coast of Española and in a few smaller inland colonies with access to south-facing, wind-aided take-off areas (Anderson et al. 2003a). We used data from 69 adults sampled at three coastal breeding subcolonies in late June–July 2000 to examine the extent of population genetic structure across the island (Fig. 1). During the breeding season we captured adults by hand and obtained small blood samples (100 μL) using brachial venipuncture. We stored blood samples in a lysis buffer (Longmire et al. 1988) for DNA extraction and genetic analysis. We sampled all adults present at Punta Suárez on 12 July 2000 ($n = 17$) and at the western extent of the Southeast Coast colony on 30 June and 4 July 2000 ($n = 22$). These sample sizes were relatively small because breeding birds typically vacate the colony after a failed breeding attempt and may not return until the next breeding season; breeding failure appeared to be relatively high at these sites in 2000 so many individuals were unavailable for sampling. The third subcolony, located near Punta Cevallos, was the focus of an intensive three-year behavioral study during the annual breeding seasons of 2000, 2001, and 2002 (Huyvaert et al., in press). Because we had taken blood samples from adults in this study area during banding efforts in 1999 and 2000, we randomly chose 30 adults observed breeding in 2000 for genetic analyses presented here.

After incubation overnight at 65°C with 300 μg Proteinase K, DNA was extracted from samples using several exchanges of phenol and phenol: chloroform:isoamyl alcohol followed by overnight dialysis against TNE_2 (Sambrook et al. 1989). We determined genotypes for sampled individuals at four polymorphic microsatellite loci (*De3*, *Dc5*, *De11*, and *Dc27*) originally isolated from Grey-headed (*Diomedea chrysostoma*) and Wandering Albatrosses (*Diomedea exulans*, Burg 1999). Polymerase chain reaction (PCR) amplification followed the two-step annealing procedure and reaction conditions outlined by Burg (1999), with slight modifications to the amplification methods. Specifically, we prepared 9.45 μL reactions including 60 ng whole genomic DNA, 10× reaction buffer, 1 mM dNTPs, 50 mM $MgCl_2$, 0.5 μg of each primer, and 0.15 U Bioline Red *Taq* DNA polymerase (Biolase, Canton, Massachusetts). PCR products were separated on 7.5% polyacrylamide gels followed by ethidium bromide staining and digital imaging. We repeated 4–6 individuals per locus on each gel to serve as size standards for comparison across gels during manual scoring. Although we used whole genomic DNA, we ran a second amplification for individuals that were initially scored as homozygotes to avoid underestimating heterozygosity due to allelic dropout (Taberlet et al. 1996, Taberlet and Luikart 1999).

We assessed deviations from Hardy-Weinberg and linkage equilibria for the four loci based on 1000 randomizations of the data and log-likelihood ratio *G*-tests for statistical significance implemented in program FSTAT version 2.9.3.2 (Goudet 1995). To describe genetic variation for each locus and subpopulation, we tabulated the number of alleles scored, estimates of allelic richness (using rarefaction procedures to account for uneven sample sizes; El Mousadik and Petit 1996, Petit et al. 1998), and Nei's unbiased gene diversity, a measure of heterozygosity (Nei 1973, 1987, Nei and Chesser 1983). Sequential Bonferroni corrections were applied in cases of simultaneous multiple comparisons of the data (Rice 1989).

We evaluated the degree of genetic differentiation among subpopulations in three ways. Differences in homogeneity of allele frequencies between pairs of sampled subcolonies were tested using nonparametric

TABLE 1. Genetic diversity based on microsatellite data at four loci for three subcolonies of Waved Albatrosses (*Phoebastria irrorata*) sampled on Española, Galápagos, Ecuador. The total number of individuals genotyped (n) is given in parentheses. The total number of alleles (N), Nei's (1973, 1987, Nei and Chesser 1983) unbiased gene diversity (h), and estimates of allelic richness (R_S for each subcolony and locus, R_T over all subcolonies) are reported for each locus and subcolony. Private alleles are indicated, with * designating one allele unique to this locus–subcolony pairing and ** designating two unique alleles.

	Punta Suárez (n = 17)			Southeast Coast (n = 22)			Study Area (n = 30)			Total (n = 69)		
Locus	N	h	R_S	N	h	R_S	N	h	R_S	N	h mean	R_T
De3	3	0.39	3.00	4	0.17	3.39	4*	0.43	3.44	5	0.33	3.44
Dc5	4	0.46	4.00	6*	0.64	5.47	5	0.60	4.67	6	0.57	4.74
De11	7**	0.75	6.88	5	0.80	5.00	5	0.77	4.79	7	0.77	5.35
Dc27	3	0.44	3.00	4*	0.39	3.91	3	0.46	2.96	4	0.43	3.35
All loci	17	–	–	19	–	–	17	–	–	22	–	–
Mean	4.3	0.51	4.22	4.8	0.50	4.44	4.3	0.57	3.97	5.5	0.53	4.22

exact tests of probability distributions from the Markov chain method implemented in GENEPOP version 3.2 (Raymond and Rousset 1995a). These tests are robust and accurate for small sample sizes and provide tests of differentiation at each locus separately, allowing for detection of loci subject to selection or other effects (Raymond and Rousset 1995b). We also tested the hypothesis of no allele frequency differences among any locus–subcolony groupings using Fisher's combined chi-square test, which has been shown to be a more powerful method when examining genetic differentiation by comparing differences in allele frequencies (Ryman and Jorde 2001). Software program FSTAT was used to estimate values of the F_{ST} variant, θ (Weir and Cockerham 1984), for all pairs of subcolonies. The F_{ST} estimator that we applied, θ, gives a measure of the degree of divergence among a set of subpopulations while accounting for variable sample and population sizes; as the value of θ approaches zero, it indicates an even distribution of alleles among sites relative to the population as a whole (Weir and Cockerham 1984, Weir 1996). Permutation tests of the hypothesis of evenly distributed allele frequencies among sites (no genetic differentiation) were performed with 60 permutations of the dataset, the number determined to be necessary by FSTAT. Lastly, because no clear consensus has been reached about the most appropriate mutation model for microsatellites (Balloux and Goudet 2002), we also report Slatkin's (1995) measure of population genetic structure, R_{ST}, which is calculated assuming a strict stepwise-mutation model for microsatellites. R_{ST} values were estimated following Rousset (1996) and Goodman (1997).

RESULTS

GENETIC DIVERSITY

We determined genotypes for all 69 individuals sampled from the three sites for three of the four loci and genotyped 67 individuals at the fourth locus, *Dc5*. We did not detect any departures from Hardy-Weinberg equilibrium in the 12 locus–subcolony combinations after 240 permutations ($P > 0.09$ for all combinations) and found no evidence of linkage disequilibrium among pairs of loci after correcting for multiple comparisons (120 permutations, $P > 0.03$ in all cases, critical value = 0.008). Four to seven alleles for each microsatellite locus and a total of 22 different alleles across the four loci were identified; five of these alleles were noted as private alleles unique to a single locus–subcolony pairing (Table 1). Estimates of allelic richness differed slightly among loci where estimates for locus *De11* were higher across the total dataset and for two of the three subcolonies individually (Table 1), although estimates of richness did not differ significantly among the three populations given the small number of loci (Friedman's test, $\chi^2_2 = 1.5$, $P = 0.47$). Similarly, gene diversity estimates were typically higher for locus *De11* (Table 1) but did not differ from one subcolony to the next (Friedman's test, $\chi^2_2 = 2.0$, $P = 0.37$).

POPULATION GENETIC STRUCTURE

Applying nonparametric exact tests implemented in GENEPOP, we found that the distribution of alleles in our sampled subcolonies did not differ for any pair of subcolonies at any locus after correction for multiple comparisons ($P > 0.04$ in all cases, critical value = 0.017 for each locus). Similarly, there was no evidence of genetic differentiation across all subpopulations at each locus ($P > 0.06$ in all cases) or for all loci combined (Fisher's combined $\chi^2_8 = 10.3$, $P = 0.24$). We also did not detect significant population genetic differentiation using Weir and Cockerham's (1984) F_{ST} variant, θ. Our highest pairwise value of θ was 0.012 between the Southeast Coast and Punta Suárez subcolonies and no pairwise test of genetic differentiation was statistically significant ($P > 0.18$ for all comparisons; Table 2). Lastly, R_{ST} estimates over all sampled subcolonies for each locus ranged from –0.009 (*De11*) to 0.06 (*De3*) and R_{ST} over all loci and subcolonies was 0.015.

DISCUSSION

Dispersal and mate choice behaviors have important consequences for population genetic structure because these behaviors in large part determine the spatial and temporal distribution of alleles. Recent work advocates integrating data from both popula-

TABLE 2. Estimates of genetic differentiation among subcolonies of the Waved Albatross (*Phoebastria irrorata*), a single-island endemic. Pairwise values of θ (an estimate of genetic differentiation analogous to F_{ST} [Weir and Cockerham 1984]) are displayed above the diagonal and significance values for each pairwise comparison are given below the diagonal. Values of θ close to zero indicate an even distribution of alleles among sites relative to the population as a whole and thus reflect little genetic differentiation among subcolonies.

Subcolony	Punta Suárez	Southeast coast	Study area
Punta Suárez	–	0.012	–0.004
Southeast Coast	0.183	–	0.003
Study Area	0.267	0.333	–

tion genetics and behavioral ecology to better understand the distribution and dynamics of genetic variation (Sugg et al. 1996). Behavioral data suggest that Waved Albatrosses are strongly philopatric to natal and breeding sites (Harris 1973; KPH, unpubl. data). Here, we examined the hypothesis that strong philopatry would result in a nonrandom distribution of genetic variation among subpopulations of the single-island endemic Waved Albatross.

Our microsatellite data were not congruent with the expectation of population genetic differentiation among sampled subcolonies. We found no evidence of deviations from Hardy-Weinberg or linkage equilibrium conditions, suggesting an absence of nonrandom mating as well as no admixture of individuals with particular alleles or genotypes. Genetic diversity measures showed a similar absence of differentiation among subcolonies. Neither allelic richness nor gene diversity measures were significantly different among the sampled sites, again suggesting current or recent mixis. Finally, we found no evidence of genetic subdivision among the three subcolonies using any of our estimates of differentiation. As θ, the F_{ST} analog that we applied, approaches zero, it indicates a more even distribution of alleles among sites relative to the entire population (Weir and Cockerham 1984, Weir 1996). No value of θ accounting for all loci at the same time was higher than 0.012. This is in keeping with the overall R_{ST} value of 0.015 and exact-test results showing no differential distribution of alleles for any pair of subcolonies over all loci and within each locus examined separately. These data, taken together, provide strong evidence of genetic homogeneity among our sampled subcolonies.

Our data contribute to a small set of studies exploring philopatry and population genetic structure among procellariiforms, tube-nosed seabirds including shearwaters, fulmars, and albatrosses. Procellariiforms and other seabirds are often cited as archetypes of highly philopatric species (Greenwood and Harvey 1982, Warham 1996). Evidence from long-term capture-mark-recapture studies supports the generalization of high philopatry: breeding dispersal was zero in Black-browed and Grey-headed Albatrosses (Prince et al. 1994), 2.9% in Wandering Albatrosses (dispersals were <1 km in distance; Inchausti and Weimerskirch 2002), and 10%–15% of breeding adults disappeared or dispersed in Cory's Shearwaters (Ristow et al. 1990, da Silva and Granadeiro 1999). However, in conflict with this are other results from these same species: 23% of juvenile Wandering Albatrosses dispersed to breed in other colonies as far as 1450 km away (Inchausti and Weimerskirch 2002), 69% of female Cory's Shearwaters returning to breed settled at subcolonies different from, although close to, their natal subcolonies (Rabouam et al. 1998), and Prince et al. (1994) estimated new recruit immigration and emigration rates to be 12%–15% for Grey-headed and Black-browed Albatrosses. Thus, an absence of strong genetic differentiation among Waved Albatross breeding subcolonies may be accounted for by low but sufficient levels of recruitment to non-natal breeding sites. Because time to recruitment in Waved Albatrosses might exceed the length of Harris's (1973) study (at most seven years between banding chicks and checking for new recruits), 93% natal philopatry could be an overestimate or, very likely, natal dispersal at this rate is sufficient to promote genetic mixing and to prevent genetic differentiation in this species.

Molecular data in other procellariiforms have shown a lack of population-level genetic differentiation and are thus also suggestive of some postfledging vagility. Both mtDNA and microsatellite analyses have shown no appreciable population structure in Grey-headed Albatrosses (Burg and Croxall 2001) and a study using minisatellites demonstrated low levels of differentiation in Cory's Shearwaters (da Silva and Granadeiro 1999). Microsatellite data on Buller's Albatrosses (*Thalassarche bulleri bulleri*) suggest that genetic homogeneity among island populations is maintained by some degree of gene flow, even in the face of apparently high natal philopatry (Van Bekkum et al. 2006). A similar lack of population-level genetic differentiation was demonstrated for White-capped Albatrosses (*Thalassarche steadi*), but not for the closely related Shy Albatross (*T. cauta*), in which longer geographic distances among populations were proposed to explain significant levels of population-level genetic differentiation (Abbott and Double 2003). Significant differentiation between populations of Black-browed Albatrosses on the Falkland Islands and those on other islands was explained by spatial differences in foraging grounds leading to demographic isolation and genetic drift for the Falkland populations (Burg and Croxall 2001).

To our knowledge, no spatial differences in foraging destination exist among our sampled subcolonies of Waved Albatrosses, but no data are available on the foraging destinations of birds from Punta Suárez or the Southeast Coast. Satellite tracking and presence/absence studies suggest that individuals from our study area near Punta Cevallos forage at close or distant sites depending on timing within their nesting phenology rather than colony

location (Anderson et al. 2003b). Given Española's small size, breeding subcolonies are not strongly geographically isolated from each other. However, our study might have been improved by comparing our data to microsatellite data from samples of the few birds that occasionally breed on distant Isla de la Plata, ~1000 km from Española (Anderson et al. 2003a). The most likely scenario, given our data, is that a small but measurable degree of natal dispersal accounts for the absence of genetic structure among subcolonies of Waved Albatrosses; conducting larger scale and longer term monitoring of banded juveniles and increasing the number of individuals of different life stages sampled might help to separate the effects of breeding and natal dispersal on population genetic structure.

We are grateful to a number of field assistants for help collecting data in all stages of this project. In particular, we thank J. L. Bollmer and H. Mouritsen for assistance collecting samples and D. J. Anderson for extensive logistical support and encouragement throughout the study. We appreciate the hard work and cheerful goodwill of K. Halbert and S. Schrock in the laboratory, and S. Siers for help redrawing Figure 1. Two anonymous reviewers provided very helpful comments for improving an earlier draft of the manuscript. Financial support came from the University of Missouri-St. Louis, the Des Lee Collaborative Vision in Zoological Studies and the International Center for Tropical Ecology at the University of Missouri-St. Louis, The Ohio State University, Sigma Xi, and Wake Forest University. This study was conducted with permission to sample and handle birds from the Galápagos National Park Service and with logistical support from the Charles Darwin Research Station and TAME airlines. All capture and sampling procedures were approved by the Institutional Animal Care and Use Committees at the Ohio State University and the University of Missouri-St. Louis.

LITERATURE CITED

ABBOTT, C. L., AND M. C. DOUBLE. 2003. Genetic structure, conservation genetics and evidence of speciation by range expansion in Shy and White-capped Albatrosses. Molecular Ecology 12: 2953–2962.

ANDERSON, D. J., K. P. HUYVAERT, V. APANIUS, H. TOWNSEND, C. L. GILLIKIN, L. D. HILL, F. JUOLA, E. T. PORTER, D. R. WOOD, C. LOUGHEED, AND H. VARGAS. 2003a. Population size and trends of the Waved Albatross *Phoebastria irrorata*. Marine Ornithology 30:63–69.

ANDERSON, D. J., K. P. HUYVAERT, D. R. WOOD, C. L. GILLIKIN, B. J. FROST, AND H. MOURITSEN. 2003b. At-sea distribution of Waved Albatrosses and the Galápagos Marine Reserve. Biological Conservation 110:367–373.

BALLOUX, F., AND J. GOUDET. 2002. Statistical properties of population differentiation estimators under stepwise mutation in a finite island model. Molecular Ecology 11:771–783.

BURG, T. M. 1999. Isolation and characterization of microsatellites in albatrosses. Molecular Ecology 8:335–340.

BURG, T. M., AND J. P. CROXALL. 2001. Global relationships amongst Black-browed and Grey-headed Albatrosses: analysis of population structure using mitochondrial DNA and microsatellites. Molecular Ecology 10:2647–2660.

CHESSER, R. K. 1991. Influence of gene flow and breeding tactics on gene diversity within populations. Genetics 129:573–583.

DA SILVA, M. C., AND J. P. GRANADEIRO. 1999. Genetic variability and isolation of Cory's Shearwater colonies in the northeast Atlantic. Condor 101:174–179.

DIECKMANN, U., B. O'HARA, AND W. WEISSER. 1999. The evolutionary ecology of dispersal. Trends in Ecology & Evolution 14:88–90.

DOUGLAS, H. D. 1998. Changes in the distribution and abundance of Waved Albatrosses at Isla Española, Galápagos Islands, Ecuador. Condor 100:737–740.

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

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

GOODMAN, S. J. 1997. R_{ST} Calc: a collection of computer programs for calculating estimates of genetic differentiation from microsatellite data and determining their significance. Molecular Ecology 6:881–885.

GOUDET, J. 1995. FSTAT (v. 1.2): a computer program to calculate *F*-statistics. Journal of Heredity 86:485–486.

GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. Annual Review in Ecology and Systematics 13:121.

HARRIS, M. P. 1973. The biology of the Waved Albatross *Diomedea irrorata* of Hood Island, Galápagos. Ibis 115:483–510.

HUYVAERT, K. P., D. J. ANDERSON, AND P. G. PARKER. In press. The mate opportunity hypothesis and extra-pair paternity in Waved Albatrosses (*Phoebastria irrorata*). Auk.

INCHAUSTI, P., AND H. WEIMERSKIRCH. 2002. Dispersal and metapopulation dynamics of an oceanic seabird, the Wandering Albatross, and its consequences for its response to long-line fisheries. Journal of Animal Ecology 71:765–770.

LONGMIRE, J. L., A. K. LEWIS, N. C. BROWN, J. M. BUCKINGHAM, L. M. CLARK, M. D. JONES, L. J. MEINCKE, J. MEYNE, R. L. RATLIFF, F. A. RAY, R. P. WAGNER, AND R. K. MOYZIS. 1988. Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. Genomics 2:14–24.

MOUQUET, N., G. S. E. E. MULDER, V. A. A. JANSEN, AND M. LOREAU. 2001. The properties of competitive communities with coupled local and regional dynamics, p. 311–326. *In* J. Clobert, E.

Danchin, A. A. Dhondt, and J. D. Nichols [EDS.], Dispersal. Oxford University Press, New York.

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

NEI, M. 1987. Molecular evolutionary genetics. Columbia University Press, New York.

NEI, M., AND R. K. CHESSER. 1983. Estimation of fixation indices and gene diversities. Annals of Human Genetics 47:253–259.

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.

PRINCE, P. A., P. ROTHERY, J. P. CROXALL, AND A. G. WOOD. 1994. Population dynamics of Black-browed and Grey-headed Albatrosses *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. Ibis 136:50–71.

RABOUAM, C., J.-C. THIBAULT, AND V. BRETAGNOLLE. 1998. Natal philopatry and close inbreeding in Cory's Shearwater (*Calonectris diomedea*). Auk 115:483–486.

RAYMOND, M., AND F. ROUSSET. 1995a. GENEPOP (v. 1.2): a population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

RAYMOND, M., AND F. ROUSSET. 1995b. An exact test for population differentiation. Evolution 49: 1280–1283.

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

RISTOW, D., F. FELDMANN, W. SCHARLAU, AND M. WINK. 1990. Population structure, philopatry and mortality of Cory's Shearwater *Calonectris diomedea diomedea*. Die Vogelwelt 111:172–181.

ROUSSET, F. 1996. Equilibrium values of measures of population subdivision for stepwise mutation processes. Genetics 142:1357–1362.

RYMAN, N., AND P. E. JORDE. 2001. Statistical power when testing for genetic differentiation. Molecular Ecology 10:2361–2373.

SAMBROOK, J., E. F. FRITSCH, AND T. MANIATIS. 1989. Molecular cloning: a laboratory manual. Cold Spring Harbor Press, Cold Spring Harbor, NY.

SLATKIN, M. 1995. A measure of population subdivision based on microsatellite allele frequencies. Genetics 139:457–462.

SPONG, G., J. STONE, S. CREEL, AND M. BJORKLUND. 2002. Genetic structure of lions in the Selous Game Reserve: implications for the evolution of sociality. Journal of Evolutionary Biology 15:945–953.

SUGG, D. W., R. K. CHESSER, F. S. DOBSON, AND J. L. HOOGLAND. 1996. Population genetics meets behavioral ecology. Trends in Ecology & Evolution 11:338–342.

TABERLET, P., S. GRIFFIN, B. GOOSENS, S. QUESTIAU, V. MANCEAU, N. ESCARAVAGE, L. P. WAITS, AND J. BOUVET. 1996. Reliable genotyping of samples with very low DNA quantities using PCR. Nucleic Acids Research 26:3189–3194.

TABERLET, P., AND G. LUIKART. 1999. Non-invasive genetic sampling and individual identification. Biological Journal of the Linnean Society 68: 41–55.

VAN BEKKUM, M., P. M. SAGAR, J.-C. STAHL, AND G. K. CHAMBERS. 2006. Natal philopatry does not lead to population genetic differentiation in Buller's Albatross (*Thalassarche bulleri bulleri*). Molecular Ecology 15:73–79.

WARHAM, J. 1996. The behaviour, population biology and physiology of the petrels. Academic Press, London.

WEIR, B. S. 1996. Genetic data analysis II. Sinauer Associates, Inc., Sunderland, MA.

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