Molecular Ecology (2003) **12**, 2835–2843 doi: 10.1046/j.1365-294X.2003.01931.x

Inter-island movements and population differentiation in a pelagic seabird

DONALD C. DEARBORN,* ANGELA D. ANDERS,† E. A. SCHREIBER,‡ RACHELLE M. M. ADAMS§ and ULRICH G. MUELLER§

**Department of Biology and Program in Animal Behaviour, Bucknell University, Lewisburg PA 17837, †Program in Ecology, Pennsylvania State University, University Park, PA 16802, ‡National Museum of Natural History, MRC 116, Smithsonian Institution, Washington DC 20560, §Section of Integrative Biology, University of Texas, Austin TX 78712*

Abstract

We used mark–resight data and amplified fragment length polymorphism (AFLP) markers to assess movements and gene flow between Central Pacific breeding colonies of the great frigatebird, *Fregata minor*. Of 715 adult frigatebirds marked on Tern Island and Johnston Atoll, 21.3% were resighted at other frigatebird colonies at least 582 km away. Mark–resight data indicated regular movement of males and females between Tern Island and Johnston Atoll (873 km apart), and less frequent movements to other islands; no birds marked on Tern or Johnston were seen on Christmas Island, but one was seen in the Philippines, 7627 km from where it was marked. Despite the regular occurrence of interisland movements, Bayesian analyses of AFLP data showed significant genetic differentiation between Tern Island and Johnston Atoll, and more pronounced differentiation between these two islands and the more distant Christmas Island. The AFLP profiles of three birds breeding on Tern Island fell within the profile-cluster typical for Christmas Island birds, both in a nonmetric multidimensional scaling analysis and in a population assignment test, suggesting dispersal events from Christmas Island to Tern Island. Several factors could explain the persistence of genetic structure despite frequent movements between colonies: many movements occurred during the nonbreeding season, many breeding-season movements did not involve mate-acquisition behaviours and individuals that do disperse may be selected against, as suggested by morphometric differences between colonies. The persistence of genetic structure among breeding colonies despite significant interisland movements suggests limits to the effectiveness of migration as a homogenizing force in this broadly distributed, extremely mobile species.

Keywords: AFLP, Bayesian, frigatebird, genetics, island, mark–resight

Received 7 March 2003; revision received 11 June 2003; accepted 11 June 2003

Introduction

Dispersal is critically linked to the demographic and evolutionary trajectories of populations (Slatkin 1987; Bohonak 1999; Ross 2001). For example, migration from source populations can sustain sink populations (Robinson *et al*. 1995), and extensive gene flow can hinder local adaptation and divergence between populations (Storfer 1999). Hence, a proper understanding of demographic and evolutionary processes within a population requires knowing the extent to which a given population interacts with others.

Across taxa, the extent of genetically effective dispersal is generally predicted by dispersal capability (Bohonak 1999). Thus, it is perplexing that in seabirds, in which wing morphology, mark–recapture data and satellite telemetry data indicate the capacity to travel enormous distances, species often exhibit strong natal site fidelity (Fisher 1976; Schreiber & Schreiber 1993; Austin *et al*. 1994; Schørring 2001; Bried & Jouventin 2002). For example, despite the fact that Laysan albatrosses (*Diomedea immutabilis*) fly routinely on foraging trips in excess of 2000 km between bouts of chick-feeding (Fernández *et al*. 2001),

Correspondence: Don Dearborn, Department of Biology and Program in Animal Behaviour, Bucknell University, Lewisburg PA 17837, USA. Fax: 570-577-3537; ddearbor@bucknell.edu

individuals breed typically within 30 m of their natal nest (Fisher 1976).

The long-distance movements of breeding seabirds revealed by satellite telemetry (Jouventin & Weimerskirch 1990; Weimerskirch *et al*. 1993; Weimerskirch *et al*. 1994; Berrow & Wood 2000; Catard *et al*. 2000; Hamer *et al*. 2001; Quintana & Dell'Arciprete 2002) clearly have no impact on gene flow, as these movements involve the foraging journeys of birds that are already engaged in a breeding attempt. In contrast, local resight data at a breeding colony of great frigatebirds (*Fregata minor*) on Tern Island, Hawaii, showed a frequent turnover among adults that were at the colony but not currently breeding there (Wise, Hull, Dearborn & Anders, in prep.). In addition, recent satellite telemetry of magnificent frigatebirds (*F. magnificens*) has shown the capacity for long-distance movements in this genus (Weimerskirch *et al*. 2003), although as with studies of albatrosses, the birds in that study were breeders engaged in central-place foraging. If the frequent turnover of prebreeding or postbreeding birds within a colony is indicative of movement between breeding colonies rather than foraging trips with an eventual return to the same island, there exists the potential for effective dispersal and gene flow in frigatebirds and perhaps other pelagic seabirds.

In this study, we used two approaches to assess the movement of great frigatebirds between islands. First, we used mark–resight data to test whether great frigatebirds visit breeding colonies on multiple islands. Second, we used amplified fragment length polymorphism (AFLP) data to test whether colonies on different islands are genetically homogeneous; that is, whether long-distance movements result in effective gene flow between spatially disjunct breeding colonies.

Materials and methods

Study species and population

Great frigatebirds (*Fregata minor*) are pelagic seabirds that breed on remote islands in the Pacific and Indian Oceans (Nelson 1975). Frigatebirds have a lek-like mating system featuring male sexual ornaments, extensive female mate choice and pair bonds that last for only a single breeding attempt (Dearborn *et al*. 2001; Dearborn & Ryan 2002). During the breeding season, male frigatebirds perch in bushes to perform courtship displays while females fly over the breeding colony in the initial stages of choosing a mate (Nelson 1975). Both sexes share in parental care (incubation, chick-brooding and chick-feeding) during a breeding effort that lasts nearly a year (Nelson 1975; Dearborn 2001). Our study population occurs in French Frigate Shoals, a 29-km wide atoll in the Northwestern Hawaiian Islands; among the dozen small islands that constitute French Frigate Shoals, frigatebirds currently breed only on 14-ha Tern Island. In this breeding colony, pair formation and nest initiation occur from January to April. During this time, large numbers of unpaired birds gather on the island (Dearborn *et al*. 2001) and these individuals vary extensively in the duration of their stay on the island (Wise, Hull, Dearborn & Anders, in prep.). Peak 1-day counts of frigatebirds on Tern Island reveal approximately 2600 individuals at a time (not accounting for turnover of individuals), and there are roughly 1500 nest attempts each season. Populations are smaller on Johnston Atoll and Christmas Island, with 150 and 500 annual nest attempts, respectively, and roosting populations up to 2000 (E. A. Schreiber, unpubl. data).

Mark–resight data

We banded great frigatebirds with numbered leg bands and, in order to resight birds without recapture, we used patagial tags made of a reinforced vinyl (Roadway™). Tags were wrapped around the radius/ulna, with a narrow piece sliding between two secondary feathers and connecting to an interlocking tab (Osorno 1999). Tags were marked on both sides with a unique three-character code. An identical tag was placed on each wing to facilitate identification of a perched bird from either side and to assess the rate of tag loss.

We used yellow material because this was seen readily in the field but had no obvious ecological relevance to the birds (i.e. was not red of male throat pouch, or pink of female eye ring, or white of juvenile under-wing feathers). Adult frigatebirds have no predators, so there is no predation-risk imposed by a bright yellow tag.

We marked adult great frigatebirds on Tern Island in 1998, 1999 and 2000, and on Johnston Atoll in 1999 (Fig. 1). Birds were marked between January and June and consisted of a mix of breeders and birds not known to breed in the year they were marked. A total of 657 adults were wing-tagged on Tern Island (300 in 1998, 224 in 1999 and 133 in 2000). In 1999, 58 adults were wing-tagged on Johnston Atoll.

Resighting surveys were conducted in two ways: regular census and opportunistic observation. On Tern Island, the colony was censused regularly during the breeding season. In 1998, surveys were conducted daily from 15 January to 15 July at 17 : 00. In 1999, surveys were conducted daily from 20 January to 2 May at 11 : 30 and 17 : 00. In 2000, surveys were made daily from 21 January to 15 May at 09 : 00, 13 : 30 and 17 : 00. Surveys for marked birds were made by walking a regular route around the breeding colony, and our search path was never more than 50 m from the birds that we were counting. Frigatebirds are large animals (2 m wingspan) that perch on the tops of low bushes (generally 1–2 m high), and Tern Island is treeless and sparsely vegetated. In addition, the yellow patagial tags contrast sharply with the birds' black wings. Lastly, 94% of on-island adults were perched rather than flying around

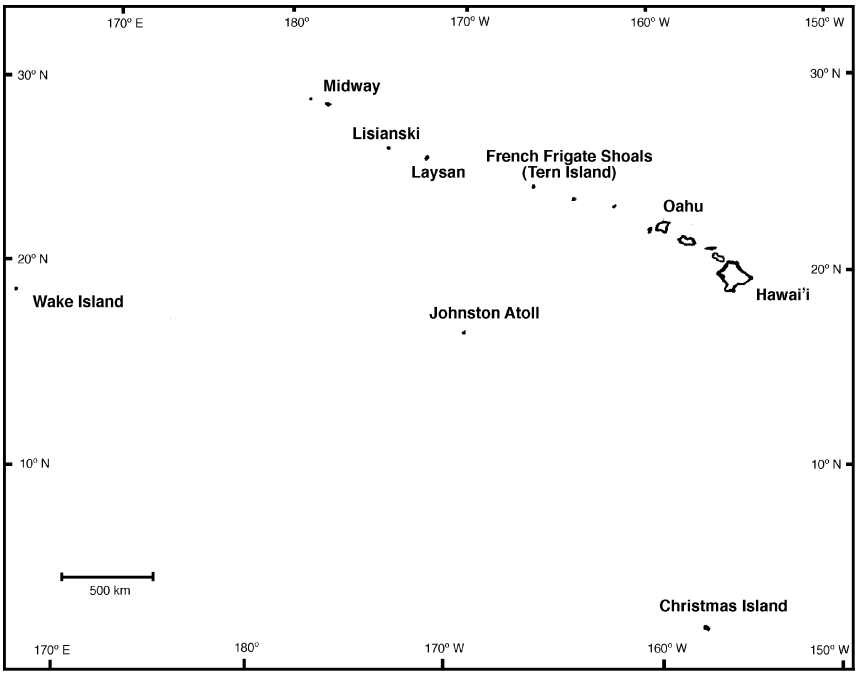

Fig. 1 Frigatebirds were marked with wing tags on Tern Island (in the small atoll of French Frigate Shoals) and Johnston Atoll in the Central Pacific. Blood samples were collected from breeding populations on Tern Island, Johnston Atoll and Christmas Island.

the island during our surveys (Dearborn *et al*. 2001). The combination of these factors made detection of marked individuals very easy.

On other islands, information was gathered opportunistically by various researchers (primarily employees of the US Fish and Wildlife Service) in response to our request for assistance. These islands included Laysan, Lisianski and Midway in the Hawaiian Archipelago, and Johnston Atoll, Wake Island and Christmas Island further south in the Central Pacific (Fig. 1).

AFLP data

DNA sampling protocols. We collected blood samples from great frigatebirds on Tern Island (21 adult females, 20 adult males), Johnston Atoll (seven adult females, seven adult males, and 17 chicks), and Christmas Island (10 adult females, 11 adult males, three chicks) during the 1998 breeding season (Fig. 1). All adults were breeding or attempting to breed, with the exception of one female on Johnston. All chicks were too young to fly and thus had hatched on that island. Blood was collected from either the brachial vein or a vein in the leg or foot. Two 50-μL blood samples per individual were stored in 500 μL of lysis buffer (Longmire *et al*. 1988).

DNA extraction and primer screening. Prior to DNA extraction, blood samples were incubated overnight at 65 °C with 200 μg proteinase K. DNA was isolated using 2 phenol extractions, 2 phenol–chloroform–isoamyl alcohol extractions and a final chloroform–isoamyl alcohol extraction. The final aqueous phase was dialysed overnight against TNE_2. DNA concentrations were quantified with spectrophotometry, and samples were run subsequently through an agarose gel to validate the concentration estimates and to assess integrity of the DNA. Extractions for all samples were performed in the same laboratory by the same people (DCD and ADA) during a single month to reduce the likelihood of extraction-related artefacts.

AFLP markers (Mueller & Wolfenbarger 1999) were generated using the PE Biosystems protocol (http://www.pebiodocs.com/pebiodocs/04303146.pdf) for regular plant genomes. All samples were given new randomly assigned identification numbers. Samples were sorted by these numbers during subsequent laboratory work, ensuring that any artefacts would not affect certain islands differentially and that the person scoring the markers was blind to the sampling location of the birds.

Restriction-ligation was conducted at 37 °C for 2 h using *Mse*I and *Eco*RI. Preselective amplification was performed with an *Mse*I complementary primer that includes the adapter sequence, the restriction site, and an additional 3′ C extension, and with an *Eco*RI complementary primer consisting of the adapter sequence, the restriction site, and an additional 3′ A extension. Selective amplification was performed with primers consisting of the adapter sequence, the restriction site sequence, and a 3′ Cxx (for *Eco*RI) or a 3′ Axx (*Mse*I). We initially screened 18 primer pairs, using 10 samples (four birds from Tern and three birds each from Johnston and Christmas). The eight most polymorphic and reliable primer combinations (CAA-AAC, CAA-ACA, CAC-ACA, CAG-ACT, CAG-AAC,

CAT-ACA, CTA-ACT, CTA-ACA) were used for subsequent analysis of all samples. Each sample was typed once with each primer combination.

Amplified fragments were separated and scored with a 36-cm capillary array on an ABI 3100 Genetic Analyser, using GENESCAN 3.1 and GENOTYPER 2.5 software. In addition, we confirmed visually all potential polymorphisms scored by GENOTYPER, both during the screening of primers and during final analysis of the full set of samples. Peaks were scored only if the height exceeded 60 relative fluorescent units (RFU); for 91% of the polymorphic markers retained for analysis, the minimum peak height across all samples exceeded 100 RFU. For analysis, we assumed that each band corresponded to a locus and that infrequent violations of this correspondence (i.e. cases of comigration of products from different loci; Rosendahl & Taylor 1997) would not cause systemic distortion of the results of correctly scored bands.

During amplification of fragments, we took several precautions to avoid artifacts. First, preselective amplification was performed in a 96-well plate using all samples at the same time. Second, samples were ordered by random ID numbers, precluding the possibility of polymerase chain reaction (PCR) artefacts affecting AFLP profiles differentially across the three populations. Third, we used PE Biosystems PCR Core Mix (P/N 402005) to ensure constant ratios of reactants. Fourth, selective amplification was performed with a 96-well plate, such that all samples were run simultaneously for a given primer combination. Fifth, all AFLP laboratory work was conducted by the same person (DCD). In addition to reducing artefacts, we avoided observer bias; because samples had been given random IDs for processing, scoring of polymorphisms was blind with respect to the island origin of the samples.

Analysis of AFLP data. To estimate population genetic parameters from AFLP information, we used a Bayesian approach recently developed by Holsinger *et al*. (2002), an approach that is not plagued by the problems of traditional methods of analyses using dominant markers. We used Hickory (Holsinger *et al*. 2002) to estimate θ^B, a Bayesian-derived analogue of F_{ST}, across all three populations and also for each pairwise combination of the three islands, using Hickory's default values to specify the prior distributions. Because of the uncertainties inherent in estimating F_{IS} analogues from dominant markers, we used the '*f*-free' analysis option in Hickory. This option yields wider 95% credible intervals for estimates of θ^B, but it avoids any potential bias that could be created by unreasonable estimates of the F_{IS} analogue, *f*. We used default values for burn-in (50 000), sampling (250 000) and thin (50). To ensure that the Markov chain Monte Carlo simulation was converging to a stationary distribution, we made five runs of each analysis.

To visualize the clustering of individuals based on genetic similarity, we used multidimensional scaling of the genetic distance data. First, we used PAUP* 4.0 (Sinauer Associates Inc., Sunderland, MA, USA) to generate Nei & Li (1979) distances between all pairs of individual birds. Second, we entered this distance matrix into SPSS10.0 for Macintosh (SPSS Inc., Chicago, IL, USA) for a nonmetric multidimensional scaling (NMDS) analysis. NMDS constructs a *n*-dimensional map of points, with the goal of minimizing the discrepancy between the matrix of 'real' genetic distances and the matrix of Euclidean distances in the *n*-dimensional space. We performed initial NMDS analyses with 1–5 dimensions to assess the improvement in stress score with additional dimensions.

Because NMDS analysis suggested that three of the sampled individuals were genetically dissimilar to the other birds breeding on the same island, we used the population allocation procedure in AFLPOP (Duchesne & Bernatchez 2002) to explore the possible origins of these birds. Assuming that all remaining birds originated on the islands where they were sampled, we used AFLPOP to calculate the relative likelihood of each putative disperser having originated on Tern Island, Johnston Atoll and Christmas Island.

Results

Mark–resight data

A total of 657 adults were wing-tagged on Tern Island, and an additional 58 adults were wing-tagged on Johnston Atoll. During subsequent resightings of 524 tagged birds (range 1–76 resightings per individual), we saw one bird with only one tag. Thus, tag loss within the 3 years of this study appears to have occurred rarely and was not a significant source of bias against resighting.

Of the 657 adults marked on Tern Island, 142 (21.6%) were resighted outside of French Frigate Shoals between May 1998 and December 2001 (Table 1). One of these birds was seen in Quezon City, Manila, in the Philippines, a distance of 7627 km from Tern Island.

Five individuals marked on Tern Island were reported on each of two different islands other than Tern: one on Johnston and Midway, two on Johnston and Laysan and two on Johnston and Wake. Among all birds seen elsewhere at least once, the mean number of days seen on any island other than Tern was 1.75 (range 1–8); some birds were resighted on consecutive days, whereas others were resighted during what were presumed to be separate visits to an island. Three of the males marked on Tern Island were noted performing courtship displays on islands other than Tern: one male displayed on both Tern and Laysan in 1999, a second male displayed on Tern and Johnston in 1999, and a third male displayed on both Tern and Johnston in 2000. There were no reports of marked females

Table 1 Of 657 adults marked on Tern Island, 142 (21.6%) were seen subsequently outside French Frigate Shoals. Five individuals were seen on two islands and thus appear in multiple cells of the table

	Johnston	Wake	Christmas	Philippines	Midway	Lisianski	Laysan
Km from Tern	873	2846	2627	7627	1204	807	582
Males seen	51	6	0	1	3	1	8
Females seen	71	2	0	0	0	1	3
Total seen	122	8	0	1	3	2	11

performing the less conspicuous mate-evaluating behaviours on islands other than the one on which they were originally marked.

Of the 58 adults that were wing-tagged at Johnston Atoll in 1999, 11 (19.0%) were resighted on Tern Island between January 1999 and May 2000. Of these 11 birds, one male was seen displaying to females, one female was seen evaluating males (she eventually nested on Tern) and the other nine birds were seen only perching. No birds marked on Johnston were reported being seen on any islands other than Johnston or Tern Island. Importantly, 10 of these 11 birds were simply roosting when they were initially tagged on Johnston during the breeding season.

AFLP data

Of our initial blood samples from 96 birds, we were able to amplify and score DNA fragments with all eight primer pairs for 95 birds; the remaining sample did not amplify well with any primers, apparently because of DNA extraction or storage problems. Thus, the individuals available for subsequent analysis included 23 birds from Christmas Island (nine adult females, 11 adult males and three chicks), 31 birds from Johnston Atoll (seven adult females, seven adult males and 17 chicks) and 41 birds from Tern Island (21 adult females and 20 adult males). We scored a total of 117 polymorphic bands for each of the 95 samples (an average of 14.6 polymorphic bands per primer system).

Based on these 117 polymorphic loci across the three populations, five runs of the *f*-free analysis in Hickory yielded an average $\theta^B = 0.267$ (range of estimates: 0.266–0.268; broadest bounds for 95% credible interval: 0.216–0.322). N_m, estimated as $0.5(1 - \theta^B)/\theta^B$, was 1.375. Pairwise estimates of θ^B (i.e. pairwise genetic distances between populations) were: Christmas–Johnston = 0.335 (range of five estimates: 0.334–0.336; broadest bounds for 95% credible interval: 0.269–0.405; 103 polymorphic loci), Christmas–Tern = 0.311 (range of five estimates: 0.310–0.311; broadest bounds for 95% credible interval: 0.247–0.379; 108 polymorphic loci), Tern–Johnston = 0.165 (range of five estimates: 0.164–0.166; broadest bounds for 95% credible interval: 0.105–0.239; 88 polymorphic loci). None of the 95% credible intervals spans zero.

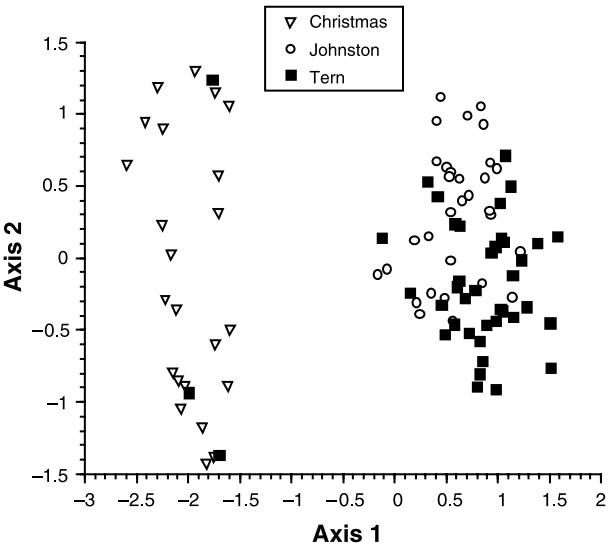

Fig. 2 Non-metric multidimensional scaling (NMDS) plot for all 95 birds, including adults and chicks. The clustering seen in this analysis was consistent with the pairwise Bayesian estimates of θ^B. Christmas–Johnston = 0.335, Christmas–Tern = 0.311 and Tern–Johnston = 0.165.

This general pattern of greater similarity between Tern and Johnston birds than to Christmas birds was also seen in the NMDS analysis (Fig. 2). Individuals sampled on Christmas Island were mostly distinct from those sampled on Tern or Johnston, although three birds sampled on Tern Island (one female, two males) fell unambiguously into the Christmas Island cluster. There was partial overlap in the general distribution of Tern and Johnston birds. The two-dimensional NMDS model shown in Fig. 2 had an S-stress of 0.216. Increasing to three dimensions yielded a slightly improved S-stress of 0.176, and a scree plot analysis indicated a decreasing rate of stress score improvement with additional dimensions.

We performed three follow-up analyses. First, because NMDS is more accurate at resolving larger distances (Borg & Groenen 1997), we re-ran the analysis of the Tern and Johnston cluster to assess better their relationships in the absence of the model-fitting effects of the Christmas Island cluster; this analysis still showed partial but not complete overlap between Tern and Johnston. Second, using all

three islands we examined breeding males and breeding females with two separate NMDS analyses to be sure there were not gross differences in patterns of among-island differentiation between genders. In this analysis, males and females exhibited similar patterns of between-island differentiation. Third, we used AFLPOP (Duchesne & Bernatchez 2002) to examine three birds that were breeding on Tern Island but whose NMDS profiles fell in the Christmas Island cluster (Fig. 2). Based on this population allocation test, these three birds breeding on Tern Island could potentially have come from any of the three islands but were > 10^5 times as likely to have originated on Christmas Island as on Tern or Johnston.

Integration of behavioural and molecular patterns

The extent to which interisland movements result in gene flow depends upon the purpose and timing of these movements. Of 248 resightings of Tern-marked birds at other colonies, 170 (68.5%) occurred outside the breeding season and eight resightings occurred on Wake Island, where frigatebirds roost but do not breed. Thus, many of these interisland movements are probably linked to seasonal migration rather than mate acquisition, and thus do not contribute to effective gene flow. However, 70 resightings of Tern-marked birds occurred during the breeding season on islands with active breeding colonies, and three adult males were documented performing courtship displays to females on multiple islands in the course of a single season. Of these three males, one individual has a relatively well-known history. He was marked on Tern Island on 28 January 1999 and was seen displaying to females on Tern each day from 29 January to 2 February; on 3 February he was seen perched on Tern. He was not seen again for 2 months. On 3 April, he was back on Tern displaying; he was seen again displaying on Tern on 4 April and 6 April. After this date he was not seen on Tern again but was seen displaying on Laysan, 582 km from Tern, on 22 April.

Other birds exhibited between-year movements. For example, a female was banded while roosting on Johnston in February 1999. She was not seen elsewhere in 1999, but she arrived at Tern Island on 9 February 2000 and evaluated prospective mates on 9–13 February, paired with a male on 14 February, and laid an egg on 20 February. The egg hatched on 15 April, and her chick was still alive when we left the island on 16 May.

Discussion

Population genetic analyses and mark–resight data on breeding colonies of great frigatebirds indicated that, although individuals move regularly between islands, genetic structure is maintained between these populations. Resight data for adult great frigatebirds marked on Tern Island and Johnston Atoll revealed extensive movements of individuals between many islands in the Central Pacific. In total, 21.4% of marked birds were subsequently resighted on other islands at least 582 km away. In particular, birds frequently moved between Tern and Johnston, a distance of 873 km: 19.0% of 58 Johnston-marked birds were later seen on Tern Island, and 18.6% of 657 Tern-marked birds were seen later on Johnston Atoll. There were relatively few sightings of marked birds further northwest in the Hawaiian Archipelago or on Wake Island. No marked birds were reported seen on Christmas Island.

The apparent lack of movement from Tern Island or Johnston Atoll to Christmas Island is not because birds are incapable of flying that far. The distances between Tern Island and Christmas Island (2627 km) and Johnston Atoll and Christmas Island (2125 km) are somewhat less than that between Tern and Wake Island (2846 km), where eight Tern-marked birds were resighted; in addition, one bird travelled 7627 km from Tern Island to the Philippines.

The rarity of sightings from Christmas Island and from the Hawaiian Archipelago may be an artefact of lower observer effort in these locations. However, band recovery data from previous studies suggest otherwise: during the 1960s, biologists with the Pacific Ocean Biological Survey Program banded over 67 000 seabirds in French Frigate Shoals (the atoll containing Tern Island) and over 200 000 seabirds elsewhere in the Hawaiian Islands and the Central Pacific (Amerson 1971). Band recoveries from great frigatebirds and other species (red-footed boobies, *Sula sula*; masked boobies, *Sula dactylatra;* sooty terns, *Sterna fuscata*) indicate that French Frigate Shoals and Johnston Atoll truly are connected by frequent interisland movements when compared to the main Hawaiian Islands, the remainder of the Northwestern Hawaiian Islands and parts of the Central Pacific (Eniwetok, Truk, Palmyra, Christmas) (Amerson 1971; Woodward 1972; Amerson & Shelton 1976; Metz & Schreiber 2002).

Population genetics analyses indicated a congruence between the frequency of interisland resights and the extent of genetic homogenization between pairs of islands, suggesting that some interisland movements result in gene flow. There was extensive overlap in the genetic clustering of birds breeding on Tern Island and birds breeding or hatched on Johnston Atoll. However, birds sampled on Christmas Island formed a very discrete genetic cluster in the NMDS analyses, suggestive of very little gene flow between Christmas Island and either Johnston or Tern. These patterns were also seen in the estimates of θ^B: overall, there was significant genetic differentiation among islands, and pairwise estimates of θ^B revealed strong differentiation between Christmas and Tern and between Christmas and Johnston, with weaker (but still significant) differentiation between the geographically closer Tern

Island and Johnston Atoll. However, the NMDS analysis and the AFLPOP allocation test revealed three birds with Christmas Island AFLP profiles breeding on Tern Island; these birds probably dispersed from Christmas to Tern Island, either as juveniles or between breeding attempts as adults. This demonstrates the potential for long-distance gene flow, despite the clear genetic clustering of Christmas Island birds.

The extent of genetic differentiation is surprising given the observed interisland movements and the genetic signatures of three dispersal events. Although the genetic and behavioural data are congruent in that the island pairs with greatest genetic similarity are also those with the greatest number of documented movements, overall there is much more genetic structure among islands than would be predicted by the frequency of interisland movements. For example, we observed 133 individuals move between Tern Island and Johnston Atoll over a period of 3 years. Given that generation time (i.e. the average reproductive age of a female) is approximately 22 years, genetic homogenization of neutral alleles would be expected across these populations if fewer than 1% of these 133 individuals were genetically effective dispersers during our 3-year study (this would correspond to a migration rate of four individuals per generation; Hartl 2000). Furthermore, the census size of the three populations and the absence of social or genetic factors that could depress the effective population size (i.e. the absence of polygamy in this species; Dearborn *et al*. 2001) both argue that the effective population size should be large enough to minimize the effects of genetic drift and allow even small selective effects to dominate over drift.

Given the overwhelming evidence for interisland movements, why do all three populations, then, exhibit pronounced genetic differentiation? One logical possibility is that most interisland movements are not related to breeding and do not result in effective gene flow. First, many of the resightings of birds (170 of 248 resightings) occurred during the nonbreeding season; these visits could have been prospecting trips to evaluate future breeding opportunities, but they would not have directly contributed to gene flow *per se*. Second, of those birds visiting other islands during the breeding season, no females were seen evaluating mates, and only a few males were recorded performing courtship displays (in total, three males were known to perform courtship displays on multiple islands in a single season). This might be an underestimate of the frequency with which birds engage in mate-acquisition behaviours on other islands, as opportunistic observations may have failed to document such behaviours; however, it seems likely that most interisland visits by frigatebirds did not involve reproductive attempts. Instead, colonies may simply be convenient stopping points when flying conditions are not favourable, as frigatebirds never land on the water (Metz & Schreiber 2002). Alternatively, these islands might be important places in which to catch thermals that may facilitate long-distance flights (Weimerskirch *et al*. 2003).

A final possibility is that selection maintains differentiation among islands despite dispersal. Overall, the patterns of genetic differentiation that we found are similar to patterns of morphometric differentiation. Based on measures of body mass, culmen length, tail length and wing length, birds differ among the three islands (Metz & Schreiber 2002), with Johnston Atoll birds typically being intermediate in size between larger birds on Tern Island and smaller birds on Christmas Island (although this pattern varies by body part). In addition, mass and culmen length are more sexually dimorphic on Christmas than on Johnston (Schreiber & Schreiber 1988). This regional variation in overall size, allometry and sexual size dimorphism could be the result of geographical variation in selection pressures or environmental influences (e.g. nutrition) affecting development. Consistent with a selection hypothesis is the lack of intermediate genotypes between Tern Island and Christmas Island despite three apparent migrants: if such dispersers were selected against after immigration, the dispersal would not act as a homogenizing force, and the genetic profiles of the populations would remain discrete. More evidvence is needed to pinpoint the factor(s) generating and maintaining genetic and morphological differentiation among these islands.

In contrast to the patterns of genetic differentiation found between populations of great frigatebirds in this study, many studies of other seabird species have found little or no population genetic structure over scales up to thousands of kilometers (Atlantic puffins *Fratercula arctica*, Moen 1991; common murres *Uria aalge*, Moum *et al*. 1991; Moum & Arnason 2001; thick-billed murres *Uria lomvia*, Birt-Friesen *et al*. 1992; short-tailed shearwaters *Puffinus tenuirostris*, Austin *et al*. 1994; imperial shags *Phalacrocorax atriceps*, Rasmussen 1994; sooty terns *Sterna fuscata*, Avise *et al*. 2000; Adelie penguins *Pygoscelis adeliae*, Roeder *et al*. 2001; ancient murrelets *Synthliboramphus antiquus*, Pearce *et al*. 2002). This absence of clear genetic differentiation sometimes occurs despite extensive natal philopatry (e.g. Moum *et al*. 1991; Austin *et al*. 1994). A subset of these studies have estimated F_{ST} or comparable statistics, and all such values are very low in comparison to those estimated here for great frigatebird populations ($\theta^B = 0.2667$, and pairwise θ^B ranging from 0.1653 to 0.3352). Comparing the extent of population differentiation across these studies must be done cautiously because of differences in genetic markers, analytical approaches and geographical scale of the study, but a coarse comparison is informative: in Adelie penguins, overall $F_{ST} = 0.0007$ based on microsatellite loci, and all pairwise F_{ST} between two populations ≤ 0.02 (Roeder *et al*. 2001); in Atlantic puffins, $F_{ST} = 0.0031$ based on allozymes (Moen 1991); in thick-billed murres, $G_{ST} = 0.001$ based on cytochrome b haplotypes (Birt-Friesen *et al*. 1992).

In contrast, other studies of seabird population genetics have found significant amounts of among-population structure (little blue penguins *Eudyptula minor*, Meredith & Sin 1988; great cormorants *Phalacrocorax carbo*, pairwise between-population R_{ST} = 0–0.195 based on microsatellite loci, pairwise between-subspecies R_{ST} = 0.097–0.212, Goostrey *et al*. 1998; marbled murrelets *Brachyramphus mamoratus*, overall ϕ_{ST} = 0.021 based on nuclear intron haplotypes, pairwise between-population ϕ_{ST} = 0–0.807, mean pairwise ϕ_{ST} = 0.062, Congdon *et al*. 2000; Cory's shearwaters *Calonectris diomedea*, F_{ST} = 0.174–0.280, depending on geographical scale of comparison, based on microsatellite fingerprinting, Rabouam *et al*. 2000; razorbills *Alca torda*, F_{ST} = 0.042 based on mtDNA control region haplotypes, Moum & Arnason 2001). However, because these studies lack critical information about the movements of individual birds, it is generally unclear whether genetic structure exists in these species as a result of restricted movements or, as seen in great frigatebirds, despite the occurrence of widespread movements between distant colonies.

Those seabird studies showing strongest genetic differentiation between populations (Congdon *et al*. 2000; Rabouam *et al*. 2000; Goostrey *et al*. 1998) varied in their implication of historical vs. contemporary processes as being responsible for current levels of differentiation, but strong fidelity to natal sites was suggested to be a potentially important force. In great frigatebirds, recoveries of birds banded as nestlings in the 1960s suggest that individuals almost always breed on their natal island (Metz & Schreiber 2002), but small-scale shifts in the location of the entire French Frigate Shoals breeding colony during the 1980s (Cohen & Dearborn, unpublished data) make it clear that site fidelity is not completely strict. In addition, many individuals banded as nestlings in the 1960s were never recaptured as adults, allowing the possibility of undetected dispersal. However, the extent of genetic differentiation observed among frigatebird populations in this study suggests that natal dispersal either does not occur often or is not genetically effective.

In conclusion, it is clear that adult great frigatebirds move regularly between breeding colonies in the Central Pacific. These movements are more extensive than those documented previously for other seabirds, yet genetic differentiation persists among these breeding colonies. Key questions remain about the forces that maintain population differentiation (for example, the role of selection perhaps operating differentially on different islands). However, this study indicates that genetic structure among populations can persist even in a species that is both broadly distributed and extremely mobile.

Acknowledgements

We thank many volunteers, especially Rachel Seabury, for extensive help with field work on Tern Island and on Johnston Atoll, and we thank Donna O'Daniel for helping to collect resighting data. The US Fish and Wildlife Service, particularly Beth Flint, kindly provided logistical support for Tern Island work and approved access to Johnston Atoll. We thank Patty Parker and her laboratory for support during DNA extraction. Thanks to Brian Wee for helpful discussions about AFLP analysis. AFLP laboratory work was funded by Seabird Research, Inc. (EAS) and NSF Career Award DEB-9983879 (UGM). We thank the Department of Defense for funding work on Johnston Atoll.

References

Amerson AB Jr (1971) The natural history of French Frigate Shoals, Northwestern Hawaiian Islands. *Atoll Research Bulletin*, **150**, 1–383.

Amerson AB Jr, Shelton PC (1976) The natural history of Johnston Atoll, Central Pacific Ocean. *Atoll Research Bulletin*, **192**, 1–479.

Austin JJ, White RWG, Ovenden JR (1994) Population-genetic structure of a philopatric, colonially nesting seabird, the short-tailed shearwater (*Puffinus tenuirostris*). *Auk*, **111**, 70–79.

Avise JC, Nelson WS, Bowen BW, Walker D (2000) Phylogeography of colonially nesting seabirds, with special reference to global matrilineal patterns in the sooty tern (*Sterna fuscata*). *Molecular Ecology*, **9**, 1783–1792.

Berrow SD, Wood AG (2000) Foraging location and range of white-chinned petrels *Procellaria aequinoctialis* breeding in the South Atlantic. *Journal of Avian Biology*, **31**, 303–311.

Birt-Friesen VL, Montevecchi WA, Gaston AJ, Davidson WS (1992) Genetic structure of thick-billed murre (*Uria lomvia*) populations examined using direct sequence analysis of amplified DNA. *Evolution*, **46**, 267–272.

Bohonak AJ (1999) Dispersal, gene flow, and population structure. *Quarterly Review of Biology*, **74**, 21–45.

Borg I, Groenen P (1997) *Modern Multidimensional Scaling: Theory and Applications*. Springer-Verlag, New York.

Bried J, Jouventin P (2002) Site and mate choice in seabirds: an evolutionary approach. In: *Biology of Marine Birds* (eds Schreiber EA, Burger J), pp. 263–305. CRC Press, Boca Raton, FL.

Catard A, Weimerskirch H, Cherel Y (2000) Exploitation of distant Antarctic waters and close shelf-break waters by white-chinned petrels rearing chicks. *Marine Ecology Progress Series*, **194**, 249–261.

Congdon BC, Piatt JF, Martin K, Friesen VL (2000) Mechanisms of population differentiation in marbled murrelets: historical versus contemporary processes. *Evolution*, **54**, 974–986.

Dearborn DC (2001) Body condition and retaliation in the parental effort decisions of incubating great frigatebirds (*Fregata minor*). *Behavioral Ecology*, **12**, 200–206.

Dearborn DC, Anders AD, Parker PG (2001) Sexual dimorphism, extrapair fertilizations, and operational sex ratio in great frigatebirds (*Fregata minor*). *Behavioral Ecology*, **12**, 746–752.

Dearborn DC, Ryan MJ (2002) A test of the Darwin–Fisher theory for the evolution of male secondary sexual traits in monogamous birds. *Journal of Evolutionary Biology*, **15**, 307–313.

Duchesne P, Bernatchez L (2002) AFLPOP: a computer program for simulated and real population allocation, based on AFLP data. *Molecular Ecology Notes*, **2**, 380–383.

Fernández P, Anderson DJ, Sievert PR, Huyvaert KP (2001) Foraging destinations of three low-latitude albatross (*Phoebastria*) species. *Journal of Zoology*, **254**, 391–404.

Fisher HI (1976) Some dynamics of a breeding colony of Laysan albatrosses. *Wilson Bulletin*, **88**, 121–142.

Goostrey A, Carss DN, Noble LR, Piertney SB (1998) Population introgression and differentiation in the great cormorant *Phalacrocorax carbo*. Europe. *Molecular Ecology*, **7**, 329–338.

Hamer KC, Phillips RA, Hill JK, Wanless S, Wood AG (2001) Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Marine Ecology Progress Series*, **224**, 283–290.

Hartl DL (2000) *A Primer of Population Genetics*. Sinauer Associates, Sundlerland, MA.

Holsinger KE, Lewis PO, Dey DK (2002) A Bayesian approach to inferring population structure from dominant markers. *Molecular Ecology*, **11**, 1157–1164.

Jouventin P, Weimerskirch H (1990) Satellite tracking of wandering albatrosses. *Nature*, **343**, 746–748.

Longmire JL, Lewis AK, Brown NC *et al.* (1988) Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. *Genomics*, **2**, 14–24.

Meredith MAM, Sin FYT (1988) Genetic variation of four populations of the little blue penguin *Eudyptula minor*. *Heredity*, **60**, 69–76.

Metz VG, Schreiber EA (2002) Great Frigatebird (*Fregata minor*). In: *The Birds of North America*, no. 681 (eds Poole A, Gill F). Academy of Natural Sciences, Philadelphia/American Ornithologists' Union, Washington, DC.

Moen SM (1991) Morphology and genetic variation among breeding colonies of the Atlantic puffin *Fratercula arctica*. *Auk*, **108**, 755–763.

Moum T, Arnason E (2001) Genetic diversity and population history of two related seabird species based on mitochondrial DNA control region sequences. *Molecular Ecology*, **10**, 2463–2478.

Moum T, Erikstad KE, Bjorklid E (1991) Restriction fragment analysis of mitochondrial DNA in common murres *Uria aalge* from four Norwegian seabird colonies. *Canadian Journal of Zoology*, **69**, 1577–1584.

Mueller UG, Wolfenbarger LL (1999) AFLP genotyping and fingerprinting. *Trends in Ecology and Evolution*, **14**, 389–394.

Nei M, Li W-H (1979) Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proceedings of the National Academy of Sciences USA*, **76**, 5269–5273.

Nelson JB (1975) The breeding biology of frigatebirds: a comparative review. *Living Bird*, **14**, 113–155.

Osorno J-L (1999) Offspring desertion in the magnificent frigatebird: are males facing a trade-off between current and future reproduction? *Journal of Avian Biology*, **30**, 335–341.

Pearce RL, Wood JJ, Artukhin Y *et al.* (2002) Mitochondrial DNA suggests high gene flow in ancient murrelets. *Condor*, **104**, 84–91.

Quintana F, Dell'Arciprete OP (2002) Foraging grounds of southern giant petrels (*Macronectes giganteus*) on the Patagonian shelf. *Polar Biology*, **25**, 159–161.

Rabouam C, Bretagnolle V, Bigot Y, Periquet G (2000) Genetic relationships of Cory's shearwaters: parentage, mating assortment, and geographic differentiation revealed by DNA fingerprinting. *Auk*, **117**, 651–662.

Rasmussen PC (1994) Geographic variation in morphology and allozymes of South American imperial shags. *Auk*, **111**, 143–161.

Robinson SK, Thompson FR III, Donovan TM, Whitehead DR, Faaborg J (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**, 1987–1990.

Roeder AD, Marshall RK, Mitchelson AJ *et al.* (2001) Gene flow on the ice: genetic differentiation among Adelie penguin colonies around Antarctica. *Molecular Ecology*, **10**, 1645–1656.

Rosendahl S, Taylor JW (1997) Development of multiple genetic markers for studies of genetic variation in arbuscular mycorrhizal fungi using AFLP. *Molecular Ecology*, **6**, 821–829.

Ross KG (2001) Molecular ecology of social behaviour: analyses of breeding systems and genetic structure. *Molecular Ecology*, **10**, 265–284.

Schørring S (2001) Ecologically determined natal philopatry within a colony of great cormorants. *Behavioral Ecology*, **12**, 287–294.

Schreiber EA, Schreiber RW (1988) Great frigatebird size dimorphism on two Central Pacific atolls. *Condor*, **90**, 90–99.

Schreiber EA, Schreiber RW (1993) Red-tailed tropicbird (*Phaethon rubricauda*). In: *The Birds of North America*, no. 43 (eds Poole A, Gill F). Academy of Natural Sciences, Philadelphia/The American Ornithologists' Union, Washington, DC.

Slatkin M (1987) Gene flow and the geographic structure of natural populations. *Science*, **236**, 787–792.

Storfer A (1999) Gene flow and local adaptation in a sunfish–salamander system. *Behavioral Ecology and Sociobiology*, **46**, 273–279.

Weimerskirch H, Chastel O, Ackermann L *et al.* (1994) Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour*, **47**, 472–476.

Weimerskirch H, Chastel O, Barbraud C, Tostain O (2003) Frigatebirds ride high on thermals. *Nature*, **421**, 333–334.

Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P (1993) Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk*, **110**, 325–342.

Woodward PW (1972) The natural history of Kure Atoll, Northwestern Hawaiian Islands. *Atoll Research Bulletin*, **164**, 1–318.

This work is part of a broader project on frigatebird mating systems in Don Dearborn's laboratory. His other interests include brood parasitism, cooperation and conflict and avian conservation. Angela Anders is an ecologist and conservation biologist who studies avian population dynamics and habitat use. E. A. Schreiber studies the ecology, breeding biology, demography and energetics of tropical Pelecaniformes and terns. Rachelle Adams is a behavioural and molecular ecologist working in the laboratory of UGM. Ulrich Mueller is interested in behavioural ecology, molecular ecology, chemical ecology and evolution.
