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GENETIC VARIABILITY AND ISOLATION OF CORY'S SHEARWATER COLONIES IN THE NORTHEAST ATLANTIC[1]

MÓNICA CARNEIRO DA SILVA[2]
Departamento Zoologia e Antropologia, Universidade de Lisboa, 1700 Lisboa, Portugal

JOSÉ PEDRO GRANADEIRO
Instituto da Conservação da Natureza, Rua Ferreira Lapa, 38-6°, 1150 Lisboa, Portugal, and Applied Ornithology Unit, Glasgow University, Glasgow G128QQ, Scotland, UK

Abstract: DNA fingerprinting was used to compare levels of genetic variability within and among eight colonies of Cory's Shearwater (*Calonectris diomedea borealis*) in the Madeira, Azores, Canarias, and Berlenga archipelagoes in the Northeast Atlantic. Fingerprint diversity, as measured by one probe and two restriction enzymes, showed very little correlation with population size, suggesting that genetic diversity reflects historical rather than current population sizes. Mean band sharing between pairs of colonies did not show any relation with between-population geographic distance. However, all between-population similarity indexes were lower than the corresponding within-population similarity index, a trend that suggests a small degree of population structure across the breeding range of this subspecies. Despite banding records suggesting high levels of philopatry, gene flow seems sufficient to prevent considerable divergence at these loci. Alternative and equally plausible explanations for the results also are discussed.

Key words: Calonectris diomedea, *Cory's Shearwater, DNA fingerprinting, gene flow, island populations, procellariiform genetic diversity.*

Avian populations are often considered an enigma with regard to degrees of geographic structure and magnitudes of gene flow. On the one hand, birds migrate long distances between breeding and wintering grounds providing substantial opportunities for admixture of populations. On the other hand, many species show a strong philopatry to breeding localities and even nest sites, and populations often exhibit geographic variation in morphological and behavioral traits, suggesting some degree of differentiation between them (Birt-Friesen et al. 1992).

Cory's Shearwater *Calonectris diomedea* is a socially monogamous species and, as most Procellariiforms, exhibits extreme demographic characteristics; it has low reproductive rates coupled with high life expectancy. The adults (over 5 years old) breed on isolated islands (the only time they come to land) sometimes in dense colonies but more often in smaller and more scattered groups (Cramp and Simmons 1977). Two subspecies are currently recognized, *C. d. borealis* breeding in the Northeast Atlantic and *C. d. diomedea* in the Mediterranean Sea. As for Cape Verde's taxon (*C. d. edwardsii*), there is increasing ev-

[1] Received 23 March 1998. Accepted 21 October 1998.

[2] Present address: Department of Zoology, Box 351800, University of Washington, Seattle, WA 98195, e-mail: mcsilva@u.washington.edu

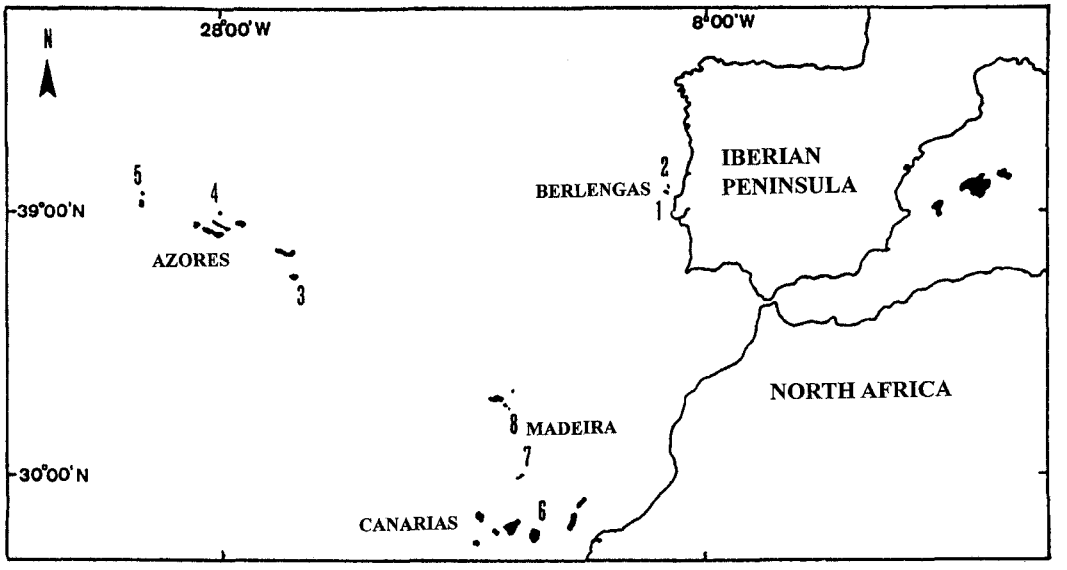

FIGURE 1. Locations of the sampled colonies of Cory's Shearwater (estimated colony sizes in parentheses). 1—Berlenga (n = 200 pairs), 2—Farilhao (n = 40 pairs), 3—Sta Maria, 4—Graciosa, 5—Corvo (for the Azores n = 49,500–89,000 pairs; Monteiro et al. 1996), 6—Alegranza (n = 8,000–10,000 pairs; Martin et al. 1991), 7—Selvagem (n = ca. 13,000 pairs), 8—Desertas (n = 1,500+ individuals; Zino and Biscoito 1994).

idence for its full species status (Hazevoet 1995, Porter et al. 1997).

The degree of genetic differentiation among populations may be determined, in part, by the magnitude of philopatric behavior exhibited by a species because it will affect the amount of gene flow between colonies and hence their degree of isolation. Recapture data of banded birds suggest that in Cory's Shearwater there is not a significant level of exchange of birds among colonies (i.e., populations) of the same subspecies (Lo Valvo and Massa 1988, Granadeiro 1991), and individuals of this species exhibit strong philopatry to their colony and even nest site (Mougin et al. 1985). Mougin et al. (1985) showed that nest fidelity of adults returning to the same colony the following year may be as high as 91%, and mate fidelity among partners returning to the colony in successive years is usually also very high (Swatschek et al. 1994). Furthermore, significant morphological differences were found within the nominal and *borealis* races (Massa and Lo Valvo 1986, Granadeiro 1993).

Multilocus DNA fingerprinting (Jeffreys et al. 1985) has proven to be an informative method to address population level questions (Triggs et al. 1992, Degnan 1993). This approach reveals restriction fragment length polymorphisms (RFLP) at hypervariable minisatellite loci that are dispersed throughout the genome (Jeffreys et al. 1985). Minisatellite DNA is not transcribed and so far no clear function has been described at the phenotypic level, thus it is reasonable to assume neutrality of the variation observed (Jarman and Wells 1989). The high rate of mutation makes minisatellites potentially of great use in addressing questions of genetic relationships among and within related populations (Degnan 1993), although the difficulty of assigning band, locus, and allele identities compromises the use of minisatellites in all but first order comparisons (Burke and Bruford 1987). In the present study, we used DNA fingerprinting to compare the genetic diversity among and within colonies of Cory's Shearwater (*Calonectris diomedea borealis*) over its breeding range in the Northeast Atlantic and to infer how genetically isolated its populations are.

METHODS

STUDY AREA AND SAMPLE COLLECTION

During the summer of 1994, 148 blood samples were collected from eight colonies comprising the breeding area of this subspecies (Fig. 1). Except for Alegranza, where only 6 samples were taken, 20 or 21 samples were collected from each colony, from either chicks and/or adults. Birds were caught by hand and blood samples of up to 1 ml were taken from the tarsus vein and immediately eluted into a lysis buffer.

LABORATORY PROCEDURES

DNA was extracted with phenol : chloroform and ethanol precipitated (Sambrook et al. 1989). For the DNA fingerprinting comparisons, 5 μg of DNA of each sample were digested overnight with excess of Pal I or Hinf I restriction enzymes, and DNA fragments were resolved in 0.8% agarose/TAE gels. Ten samples from two different populations were run in each gel along with a λHind III molecular weight marker and a control to confirm consistency of banding patterns. Gels were depurinated, denatured, and neutralized. The DNA was transferred in 20× SSC (Sambrook et al. 1989) by Southern blotting onto a nylon membrane

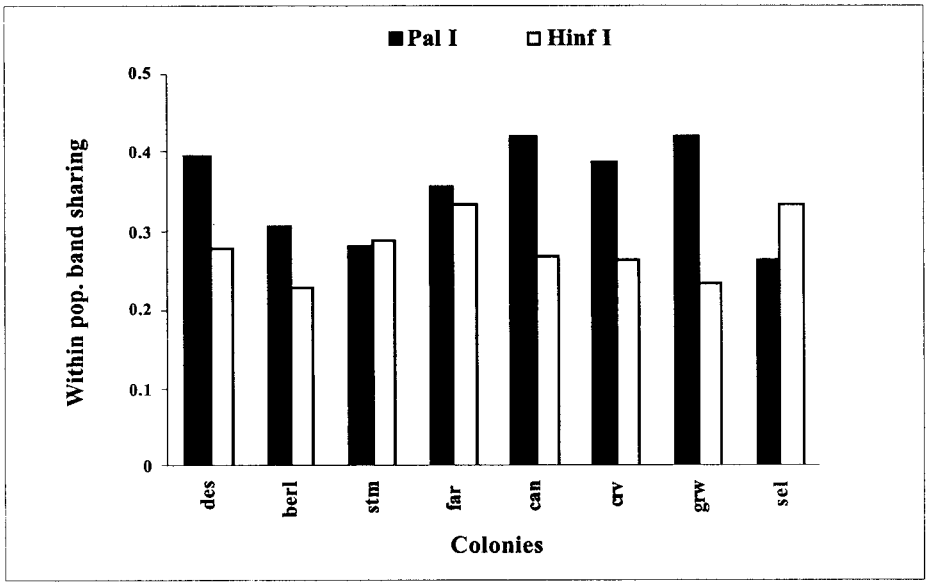

FIGURE 2. Mean within-population similarity indexes (S_{xy}) for the eight colonies of Cory's Shearwater, for each enzyme (Hinf I and Pal I). The colonies are as follows: des—Desertas, berl—Berlenga, far—Farilhao, crv—Corvo, grw—Graciosa, sel—Selvagem, stm—Santa Maria, can—Canarias Islands.

(Hybond-N$^+$, Amersham), then fixed in 0.4 M NaOH, and UV crosslinked. To generate the fingerprints, we used the radioactively-labeled pV47-2 probe (Longmire et al. 1990). Membranes were washed and exposed to X-ray film with one intensifying screen.

GENETIC ANALYSES

Gels were digitized and compared using BioImage Systems' software (version 3.2, BioImage Systems Corp., Ann Arbor, Michigan). Bands of the same size but of clearly different intensities were considered different alleles. Band intensity and a 1 mm criteria were used to differentiate the bands. Two bands were considered identical in two different individuals if they had migrated less than 1 mm apart. Only bands larger than 2.3 kb were considered in the analysis and were assumed to be unlinked. Because the control showed there was some variability associated with the migrated distance of each of its bands across gels (S_{xy} values for the same sample ran in the different gels were significantly different from 1, one sample t-test, $t_7 = 5.2$, $P < 0.002$ and $t_7 = 5.9$, $P < 0.001$ for Hinf I and Pal I, respectively), only within-gel comparisons were considered. For each gel, we calculated similarity coefficients (S) within and between populations and obtained measures of population subdivision (F_{st}) following Lynch (1990). To avoid pseudoreplication problems arising from covariation among interdependent S values, we used a subsampling routine (Danforth and Freeman-Gallant 1996) to estimate the standard error associated with each S. Statistical procedures followed Zar (1996).

RESULTS

The average number of bands per individual among the different populations was 12.3 ± 3.4 (n = 140 individuals) with Hinf I, and 13.9 ± 3.2 (n = 126 individuals) with Pal I enzyme; Pal I gave slightly higher similarity indexes over all gels (Fig. 2 and Table 1).

The overall mean within-population similarities are presented in Figure 2. The values ranged between 0.23 and 0.33 with Hinf I and between 0.26 and 0.42 with Pal I. No relation was found between the size of the populations and the similarity coefficients among their individuals ($r = 0.35$, $n = 5$, $P > 0.5$ and $r = 0.67$, $n = 5$, $P > 0.2$ for Hinf I and Pal I, respectively). Despite mean differences, the band sharing frequency distributions overlapped considerably in all colonies (data not shown), a level of resolution which does not allow assignment of individuals of unknown origin to a specific population.

Similarity indexes for the different populations are presented in Table 1. Between-population similarity indexes were consistently lower than the corresponding within-population similarity indexes, a trend which was significant for both enzymes (two-tailed paired t-test: $t_7 = 5.9$, $P < 0.001$, $t_7 = 2.6$, $P < 0.04$ for Hinf I and Pal I, respectively). No relationship was found between genetic similarity and geographic distances separating the different populations, for either of the enzymes ($r = 0.22$, $n = 8$, $P > 0.5$ and $r = 0.11$, $n = 8$, $P > 0.5$ for Pal I and Hinf I, respectively). This apparent genetic homogeneity among colonies as far as these loci are concerned is reinforced by the F_{st} values (Table 1), suggesting reduced population subdivision.

TABLE 1. Mean (± SD) similarity index ($\bar{S}$) of shearwaters' fingerprints for within and between-population comparisons using the pV47-2 probe with Hinf I or Pal I enzymes. F_{st}—estimator of population subdivision. Number of truly independent comparisons in parentheses.

Colonies	Hinf I			Pal I		
	Within-population $\bar{S}$	Between-population $\bar{S}$	F_{st}	Within-population $\bar{S}$	Between-population $\bar{S}$	F_{st}
Berlenga/Corvo	0.280 ± 0.041 (9)	0.245 ± 0.035 (9)	0.051			
Berlenga/Farilhao	0.251 ± 0.037 (10)	0.210 ± 0.026 (10)	0.053	0.292 ± 0.041 (9)	0.275 ± 0.039 (9)	0.021
Corvo/Desertas	0.264 ± 0.039 (9)	0.225 ± 0.036 (9)	0.035			
Desertas/Canarias	0.284 ± 0.036 (8)	0.259 ± 0.037 (6)	0.026	0.403 ± 0.051 (6)	0.376 ± 0.051 (6)	0.068
Farilhao/Graciosa	0.278 ± 0.031 (10)	0.211 ± 0.031 (10)	0.085			
Graciosa/Selvag.	0.323 ± 0.041 (9)	0.291 ± 0.025 (9)	0.039			
Sta. Maria/Selvag.	0.285 ± 0.046 (9)	0.207 ± 0.034 (9)	0.094	0.320 ± 0.035 (9)	0.313 ± 0.035 (9)	0.007
Sta. Maria/Canar.	0.292 ± 0.038 (8)	0.270 ± 0.041 (6)	0.020			
Berlenga/Canarias				0.378 ± 0.038 (7)	0.336 ± 0.042 (7)	0.072
Farilhao/Corvo				0.392 ± 0.039 (9)	0.270 ± 0.033 (9)	0.168
Graciosa/Canarias				0.409 ± 0.040 (8)	0.351 ± 0.041 (8)	0.078
Graciosa/Desertas				0.422 ± 0.036 (8)	0.409 ± 0.033 (8)	0.020
Sta. Maria/Selvagem				0.250 ± 0.043 (9)	0.244 ± 0.036 (9)	0.009

DISCUSSION

The observed variation in the number and distribution of bands and resulting band sharing coefficients, using different restriction enzymes, reflects variation in the frequency with which different restriction sites occur (Hanotte et al. 1992). Nonetheless, the two enzymes suggest, independently, similar conclusions.

Mean band sharing values among individuals from each colony are comparable to the highest levels of similarity reported for outbred avian populations, 0.2–0.3 (Triggs et al. 1992), but similar to the ones reported for a population of Cory's Shearwater in the Mediterranean (Swatschek et al. 1994). This fact may be explained by the highly philopatric behavior described for this species (Mougin et al. 1985, Swatschek et al. 1994), which must, to some extent, increase the proportion of matings among closely related individuals, thus decreasing the overall genetic diversity.

Genetic similarity among Cory's Shearwater populations is comparable to that found within populations of other species of birds (Burke and Bruford 1987), suggesting that between population divergence in this subspecies is low. Moreover, the band sharing coefficients revealed no correlation between the genetic divergence among populations and geographic distance. This lack of population structure is further supported by the F_{st} values which are similar to those obtained by Randi et al. (1989) in their study with the nominal subspecies, and well within the limits expected for avian species that show no strong population subdivision (Evans 1987).

There are four possible explanations for our results. First, there could be enough gene flow to prevent significant differentiation. This does not necessarily contradict the observation of significant biometric differences among colonies of Cory's Shearwater in the Atlantic (Granadeiro 1993). Slatkin (1987) suggests that natural selection can act differentially on distinct loci, causing substantial differences at a few loci which are important for local adaptations, while other loci, either neutral (as minisatellite loci) or only weakly selected, stay relatively uniform throughout a species' range. Randi et al. (1989) also proposed an interaction between selection and gene flow to explain the genetic differences between the nominal and *C. d. borealis* races. Therefore, if the morphological differences in Cory's Shearwater have a genetic basis, those loci should show a more extensive differentiation, provided that they are under substantial selection pressure. If, however, the morphological differences in this subspecies result from different ecological constraints being present in each colony, then one should not expect such a pattern. Nevertheless, this hypothesis does not agree with indirect evidence of banding data available for this subspecies (see Introduction). Moreover, we found a significant trend of lower between-population similarities in relation to the corresponding within-population similarities, which provides a hint for some genetic differentiation in Cory's Shearwater. Such an incongruence between an apparent lack of genetic structuring and indirect evidence for population differentiation has been previously described in colonial waterbirds (Friesen 1997 and references therein). In those studies, the movement of individuals among colonies was used as a likely explanation for lack of population

structuring (e.g., Heidrich et al. 1996). Although the sampled colonies are separated by distances of up to 1,900 km, it is still conceivable that low rates of gene flow, undetected with banding programs, are sufficient to maintain minisatellite alleles homogeneously spread throughout the breeding range of the subspecies.

Second, gene flow may be absent but not enough time has elapsed to allow the fixation in each colony of polymorphisms present in the ancestral population, as it has been proposed in other studies (Birt-Friesen et al. 1992, Wink et al. 1993, Heidrich et al. 1996). The recency of founder events is a less likely explanation in our case because, although these islands were affected indirectly by the climatic changes of Pleistocene, records show that there always was breeding habitat available for this subspecies throughout its range. Randi et al. (1989) acknowledged this possibility as well, although colonization of Mediterranean islands occurred only after the end of the last glaciation period. It is therefore more probable that *C. d. diomedea* populations have not achieved genetic differentiation due to recency of colony founding than for the *C. d. borealis* studied here.

Third, minisatellite loci may be evolving too rapidly and in a biased fashion, possibly resulting in convergence of minisatellite repeat number, as it has been shown for minisatellite loci of the human germ line (Jeffreys et al. 1994). If that is the case, our similarity indexes could be due to mutational biases coupled with low levels of gene flow. This possibility becomes more likely given the long divergence time of these populations on the scale of minisatellite mutation rates.

It is important to note that although mutation is a strong force shaping levels of population genetic variability, the F_{st} formula proposed by Lynch (1990) does not incorporate mutation rates. This fact may become important because if mutation rates are high, estimates of F_{st} may be underestimated given that these parameters are inversely correlated. Therefore, the fourth explanation may be that the low levels of population subdivision found result from the differentiation index we used. This hypothesis is less likely because other DNA fingerprinting studies looking at population structure of avian species (Triggs et al. 1992, Degnan 1993) showed that it is possible to find population differentiation when using Lynch's formula.

Other loci should be screened in order to measure comprehensively the levels of genetic variability and gene flow among *Calonectris diomedea borealis* populations. The spatial distribution of a single class of genetic markers often leads to incomplete "species stories" because they may retain an idiosyncratic record of evolutionary events that may differ from those of other loci.

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SYNCHRONOUS UNDERWATER FORAGING BEHAVIOR IN PENGUINS[1]

YANN TREMBLAY AND YVES CHEREL[2]
Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, F-79360 Villiers-en-Bois, France,
e-mail: cherel@cebc.cnrs.fr

Abstract. We used electronic time-depth recorders to examine the synchronous foraging behavior of penguins both at the surface and underwater. During a daily foraging trip in the chick guarding stage, two females of the Northern Rockhopper Penguin *Eudyptes chrysocome moseleyi* dove in synchrony over seven consecutive hours during which they performed together 286 dives between 3 and 60 m, and fed on the same prey, the swarming euphausiid *Thysanoessa gregaria.* Most of the synchronous dives began (71%) and ended (59%) with a time interval of ≤ 4 sec between birds. Differences in the duration and maximum depth of dives were slight: ≤ 2 sec for 44% and ≤ 1 m for 62% of the dives. Indirect evidence suggests that the two birds were part of a larger flock of foraging pen-

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[2] Corresponding author.