GEOGRAPHIC VARIATION IN THE CALL OF THE BLUE PETREL: EFFECTS OF SEX AND GEOGRAPHICAL SCALE[1]

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Abstract. We examined geographic variation between sexes in calls of Blue Petrel *Halobaena caerulea,* and at macro- (five archipelagoes) and microscales (seven islands). Using calls from 504 different individuals, we detected a significant geographic variation in males at both geographical scales, but not in females. Overall, the first syllables and silences, and some frequency parameters were highly variable between localities. In males, micro- and macroscale variations appeared equally significant, although more parameters were involved at a micro level. We discuss these results according to several hypothesis: vocal learning, environmental effect and population marker, and finally suggest that genetic drift, coupled with strong philopatry, may account for these differences.

Key words: geographic variation, vocal behavior, Blue Petrel, Halobaena caerulea.

Geographical variation in a character suggests that selective forces vary according to location (Endler 1977), and provides a key to evolutionary theory because it is linked to both adaptation and speciation (Mayr 1982). Geographic variation in birds has been studied for morphological attributes and vocalizations (Krebs and Kroodsma 1980, Zink and Remsen 1986). Most studies of geographic variation of bird vocalizations have focused on Passeriformes, particularly the oscines (Mundinger 1982, Kroodsma et al. 1984). Although they comprise half of all bird species, oscines are not necessarily representative of them, because cultural transmission of vocal characteristics is so strongly developed in this group (Kroodsma and Baylis 1982).

Petrels (Order Procellariiformes) are interesting subjects for three reasons. First, they breed on remote oceanic islands, providing natural geographic isolation which should promote geographic differentiation. Second, adults as well as fledglings are highly philopatric, as documented by banding studies (Weimerskirch et al. 1985, Thibault 1993). Geographic variation in petrels has been found in morphology (Power and Ainley 1986, Bretagnolle 1995), coloration (Ainley 1980), genetics (Randi et al. 1989, Ovenden et al. 1991), and behavior (Bretagnolle 1989, Tomkins and Milne 1991). Third, unlike in oscines, female petrels call as much as males (Bretagnolle 1996). This allows research on geographic variation in female calls, virtually unstud-

ied in birds. We examined geographic variation between sexes in calls of Blue Petrel *Halobaena caerulea,* and at macro- and microscales.

METHODS

The Blue Petrel is a medium-sized nocturnal burrow-dwelling species (average mass 200 g). At sea, it is distributed throughout the southern hemisphere, but its breeding localities are restricted to islands close to the Antarctic convergence (Fig. 1a). On Kerguelen Island (68°38'S, 48°38'E) where it is a very abundant breeding seabird, birds arrive at the colonies in September, and chicks fledge from the end of January into February.

Because of their strictly nocturnal habits, Blue Petrels (as other petrels) rely exclusively on vocalizations during pair formation (Bretagnolle 1990, Genevois and Bretagnolle 1994). Blue Petrels, as many other petrel species, use a single call, both for mating and territorial purposes (Bretagnolle 1996). There is no seasonal variation nor intra-individual variation in Blue Petrel calls (unpubl. data; see also Bretagnolle 1996 for individual stereotypy in Blue Petrel calls). Calls were recorded at night between December 1987 and January 1993 with a Nagra III or IVB tape recorder at 19.5 cm sec^{-1}, using a Sennheiser omnidirectional microphone MD 421. On Kerguelen, a total of seven different breeding islands were sampled (Fig. 1b), which allowed analysis of geographic variation at a microscale level.

Birds were recorded between November and December within their breeding burrows during a single session of one or two nights at each locality except Mayes (Kerguelen Archipelago), where recordings were gathered over several years, but in different locations of the island. Furthermore, birds were individually banded on Mayes, and the band checked after tape recording. Thus, no bird was recorded twice. Tape recordings from all other breeding localities except southern Chile (Diego Ramirez Island; Fig. 1a) also were available for comparison. A sample of 404 different males and 100 females from 11 different breeding localities were obtained. Calls were analyzed on a real time spectrograph, using a computer with an analytic package that performs a 256 points step-size fast Fourier transform (sampling rate of 6,512 Hz; Richard 1991). Frequency and temporal resolutions were respectively 13 Hz and 1 msec. In order to describe calls as fully as possible, a total of 29 parameters were measured (Fig. 2), including temporal, frequency and syntactic parameters (Genevois and Bretagnolle 1994). Temporal parameters were measured as the duration
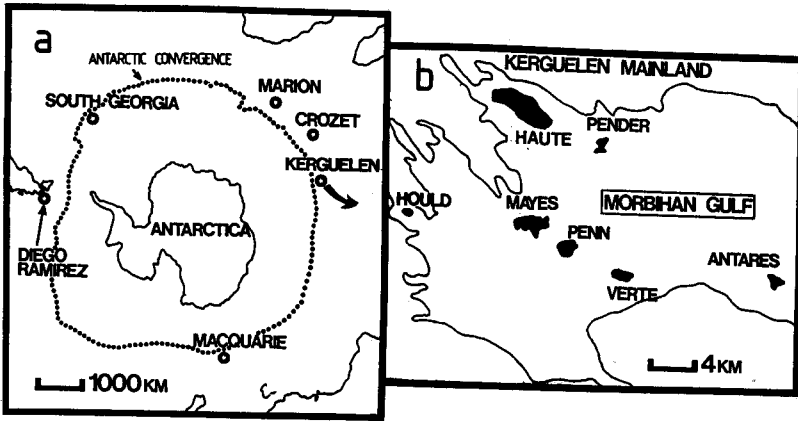
FIGURE 1.   Study area showing all localities cited in the text: (a) Southern Hemisphere (Blue Petrel distribution), with localities sampled for the study of macrogeographic variation; (b) Golfe du Morbihan, in the Kerguelen archipelago, showing the localities where microgeographic variation was studied.

(T) of the call at the beginning or the end of each syllable (Fig. 2). We then derived syllable (S) and intersyllabic (IS) durations from the differences between successive Ts.

Three types of analysis were run in which (1) the 11 localities were considered as different groups, (2) localities were combined by archipelago, and (3) the seven Kerguelen populations were considered separately. Statistical analysis involved two steps: first, considering that many acoustic parameters were intercorrelated (partly as a direct consequence of the way we measured them), we used a multivariate approach. We used Discriminant Analysis and Multiple Analysis

of Variance (MANOVA), the former giving an index of correct classification, and the latter providing multivariate statistics (Wilks' Lambda statistics). We used parametric Discriminant Analysis and two types of error rate estimates in classification: quadratic discriminant function for resubstitution, and cross-validation technique (SAS 1988). These two techniques provide lower and upper limits of error count estimates. Second, in cases where MANOVA provided significant results, we used univariate one-way Model I analysis of variance (ANOVA) with breeding locality as the factor, to identify which parameters differed significantly among localities. Given the number of tests per-
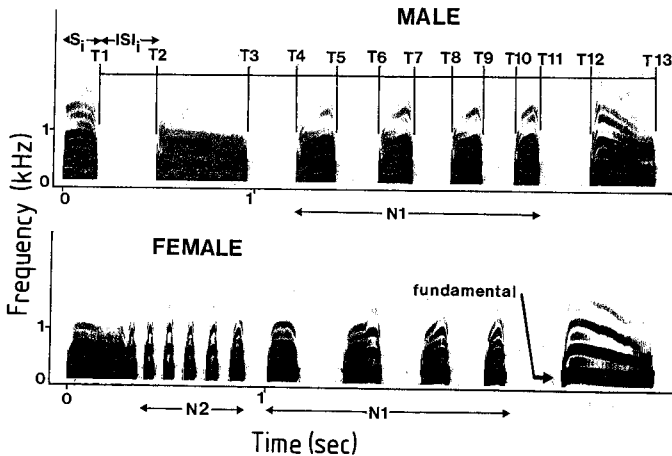

FIGURE 2.   Sonograms of a male and female Blue Petrel calls, showing the acoustic parameters that were analyzed. One syntactic (N1, number of syllables) and three frequency parameters (maximum and minimum value of the fundamental, and modal frequency) were measured in males, whereas two frequency (fundamental and modal frequencies) and two syntactic (N2, number of short syllables and N1, number of long syllables) parameters were measured in females. Time in seconds and frequency in kiloHertz. Temporal parameters, T, were measured at each beginning or end of syllable. Syllable (S) and intersyllabic (IS) durations were derived from the differences between successive Ts.

TABLE 1. Wilks' Lambda of six Multiple Analysis of Variance (MANOVA), and error rate estimates from Discriminant Analysis, performed on all acoustic parameters of Blue Petrel calls. Male and female call analysis, whether including all localities, or analyzed at the levels of micro- and macrogeographic variation are shown. When MANOVA was significant, ANOVA was performed on each acoustic parameter (rejection level of the null hypothesis has been adjusted with the Bonferroni method).

	Male			Female[a]		
	all	micro	macro	all	micro	macro
Number of localities	11	7	5	6	3	4
Number of observations	404	342	404	96	81	96
Wilks' Lambda	0.14	0.22	0.58	0.16	0.31	0.44
F-value	2.80	3.34	1.86	0.96	1.35	0.71
P	<0.001	<0.001	<0.001	0.61	0.09	0.96
Error count estimates[b] (%) (resubstitution)	7.7	8.3	0.0	—	—	—
Error count estimates[b] (%) (cross-validation)	40.3	35.4	7.7	—	—	—
Number of acoustic parameters with a significant result[c]						
Temporal parameters ($n = 25$)	15	13	3	—	—	—
Syntactic parameters ($n = 1$)	—	—	—	—	—	—
Frequency parameters ($n = 3$)	1	—	1	—	—	—

[a] Localities with only one individual were not considered.
[b] Estimated from using quadratic discriminant function.
[c] Tested using ANOVA.

formed on the same data sets, rejection level of the null hypothesis was adjusted with the Bonferroni method (Rice 1989).

RESULTS

Statistical results of six MANOVAs and Discriminant Analyses are presented in Table 1. Wilks' Lambda values (Pillai's or Hotelling traces gave the same results) were highly significant in the three analyses of males (Table 1). However, the two measures of error rate estimates were sometimes rather high (ranging from 7 to 40%; Table 1), and emphasized that although significantly variable between localities, calls also were variable within localities. Therefore, there was some overlap among populations. The situation for female calls was different, as Wilks' Lambda were not significant (Table 1), indicating that geographic variation in female calls was nonexistent. It should be noted however that microgeographic variation in female calls approached significance, and that larger sample sizes may provide different results.

Analyzing the 11 breeding localities together with ANOVA, a significant effect of locality was detected for most acoustic variables in males (Table 1). Overall, the first syllables and silences, and some frequency parameters were highly variable between localities (Fig. 3). Macro- versus microscale analyses showed different results. For instance, in males, few temporal parameters were affected by locality at a macroscale level, but the frequency parameters were (Table 1, Fig. 3). At the microscale level, the situation was nearly reversed. In males, micro- and macroscale variations appeared equally significant, although more parameters were involved at a micro level (Table 1).

DISCUSSION

Our results show that there is pronounced geographic variation in the calls of the Blue Petrel, that variation is much more pronounced in male than in female calls, and that micro- and macrogeographic variation is of similar magnitude.

Several hypotheses may explain geographic variation in bird vocalizations (reviewed in Mundinger 1982). First, geographic variation has been related to song learning (Kroodsma 1981), and viewed as non-adaptive (Baptista 1977). However, song learning is known in only four orders of birds: Passeriformes, in which it is limited to the oscines, Psittaciformes, Apodiformes, and Charadriformes (Kroodsma and Baylis 1982, Grothuis 1993). Song learning is absent in birds such as Sphenisciformes (Jouventin 1982) or Galliformes, and thus is unlikely to occur in Procellariiformes, which are close relatives to Sphenisciformes (Sibley et al. 1988). There also is indirect evidence for the nonexistence of song learning in petrels (Bretagnolle 1996), although we cannot reject that subtle adjustments might be made in calling at a given location.

Second, geographic variation in vocalizations has been related to environmental differences (Hunter and Krebs 1979), but recent experiments have provided inconclusive results (Date and Lemon 1993). Moreover, in the case of the Blue Petrel, this seems unlikely as both physical and biological acoustic environments are similar in the localities where the petrels were recorded, so that environmental effects are unlikely to have shaped vocalizations differently according to locality.

A third hypothesis, the population marker hypothesis, suggests that geographic variation in calls has the
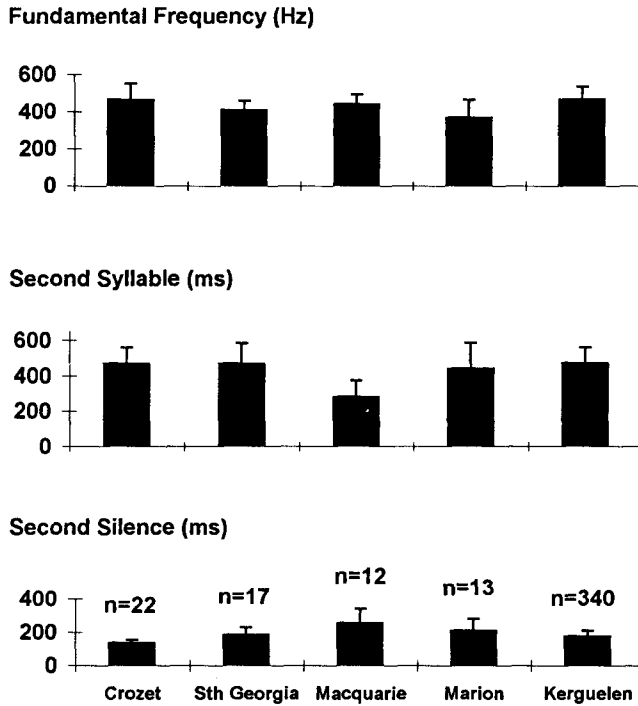
FIGURE 3:   Macrogeographic variation in the call of the Blue Petrel. Three significant acoustic parameters of Table 1 are shown, according to archipelago (means and standard deviations are given). Note scale difference between second silence and the other parameters.

function of ensuring geographic isolation between populations of a given species through assortative mating (Nottebohm 1969, Baker 1982). This latter explanation has been much debated, particularly with respect to one consequence of the population marker hypothesis: populations sharing the same songs (or dialects) would also share the same genes. This genetic corollary has been tested only in oscines with dialects: again the results were inconclusive (Baker 1982, Kroodsma et al. 1984). This may partly be due to the fact that the relationships between male dialects and female mate choice are not as direct as is usually believed, or female mate choice may rely on other cues.

Unlike oscines, nearly all species of petrels are nocturnal on their breeding colonies, and therefore rely only on acoustic signals during courtship. Calls typically are used by nonbreeding males looking for female partners, which in turn approach males and engage in duetting (James 1985, Bretagnolle and Lequette 1990). Thus, calling behavior in petrels is of prime importance in pair formation and mate choice (Storey 1984, Brooke 1990), and this applies equally to the Blue Petrel (Genevois and Bretagnolle 1994). The fact that male Blue Petrel calls vary geographically may have direct consequences for mating. Preliminary results indicate that female Blue Petrels take account of geographic variation even though there is overlap among populations (Bretagnolle et al., unpubl. data), similar to several other species where females prefer, on average, male calls from their

own geographic origin (Bretagnolle 1989, Bretagnolle and Lequette 1990, Bretagnolle et al. 1991), which is consistent with the population marker hypothesis. However, we would need to demonstrate that females actively choose mates on the basis of call characteristics with respect to geographic variation to support this hypothesis.

A last intriguing point concerns microgeographic variation in calls. Cases of variation over a few kilometers have so far been reported only in dialects of passerines (Bjorklund 1989), which cannot explain microscale variation in the Blue Petrel. We suggest that both macro- and microscale variations have the same origin, namely extreme philopatry. In the Fairy Prion *Pachyptila turtur,* a close relative to the Blue Petrel, genetic differences between populations a few kilometers apart was related to philopatry (Ovenden et al. 1991), which also may account for call differentiation. Similarly, the fact that geographic variation is nonexistent in females may be a consequence of a lesser degree of philopatry in females than in males, as reported in several petrel species (Brooke 1990, Thibault 1993).

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