SHORT COMMUNICATION

HOW USEFUL ARE VOCALIZATIONS IN PETREL SYSTEMATICS?

The taxonomic history of the order Procellariiformes has been one of conflicting and diverse opinion (Mathews 1948; Alexander et al. 1965; Sibley & Ahlquist 1972; Harper 1978; Cracraft 1981). Most studies of the group have employed traditional morphological comparisons (Murphy 1952; Murphy & Pennoyer 1952; Kuroda 1954; Bourne 1968; Harper 1980; Imber 1985) or newer biochemical ones (Sibley & Ahlquist 1972; Harper 1978; Barrowclough et al. 1981; Sibley & Ahlquist 1983). Despite the validity of these approaches, systematic problems remain, such as the relationships within the genera Pachyptila, Pterodroma, Puffinus and Pelecanoides.

Many species of the order are nocturnal at their breeding colonies, where they are highly vocal. The calls of these birds could potentially be very powerful systematic indicators, assuming that voice has risen to prominence in differentiating one species from another in the darkness of mixed species colonies. Their calls could therefore be considered good examples of ethological isolating mechanisms (Dobzhansky et al. 1977). Other authors have appreciated this in other avian taxa existing in reduced light levels (Lanyon 1969; Marshall 1978).

Attention has been paid to the use of vocal characters in avian taxanomy (Lanyon 1969; Selander 1971) and attempts have been made to compare the calls of procellariiforms (Hall-Craggs & Sellar 1976; Sparling 1977; Sparling & Williams 1978; Thibault & Holyoak 1978; Ainley 1980; Jehl 1982; Imber 1985). However, the majority of these have been inadequate because sample sizes are often small, leading to qualitative comparisons only; and account has not been taken of sexual differences in voice (Brooke 1978; Ristow & Wink 1980; James & Robertson 1985a, 1985b, 1985c). It has been suggested that such vocal comparisons not be made until the vocal characters concerned can be analysed as rigorously as more traditional mensural characters (Bourne & Jehl 1982). With this in mind, the calls and biometrics of two pairs of petrel species were compared in order to determine whether the calls were as useful as traditional morphometrics in separating the species.

METHODS

The calls and body measurements of male Manx Shearwaters *Puffinus puffinus* and Little Shearwaters *P. assimilis* were used for one comparison, and those of male British Storm Petrels *Hydrobates pelagicus* and Madeiran Storm Petrels *Oceanodroma castro* were used for the other. Calls and measurements of the Manx Shearwater and British Storm

Petrel were collected at Skomer Island, U.K. (51°45′N, 5°18′W), and those of the Little Shearwater and Madeiran Storm Petrel were collected at Great Salvage Island (30°09′N, 15°52′W) in the eastern sub-tropical Atlantic.

For the two shearwaters, four morphological variables were taken for comparison: tarsus length, bill length, wing length and body weight. Tarsus length was measured from the middle of the mid-tarsal joint to the distal end of the tarso-metatarsus; bill length was taken along the dorsal mid-line from the edge of the feathering to the tip of the hook; wing length was a flattened and straightened chord. The calls of the two species were recorded using a Uher 4000 IC tape recorder, and were always of birds calling from burrows. These were played through a Kay 6061-B Sound Spectrograph and sonagrams produced using the wide band filter. Six call variables were measured for comparison between the two species (Fig. 1).

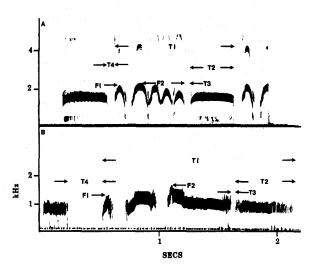


Figure 1. Sonagrams of male (A) Little Shearwater and (B) Manx Shearwater showing call variables measured: T1 = call length; T2 = breath note length; T3 = gap between breath note and rest of call; T4 = gap between successive calls; F1 = maximum frequency of introductory note; F2 = maximum frequency of whole call.

For the two storm petrels, four morphological variables were also compared: tarsus length, bill length, wing length and tail length. Tail length was measured from the tip of the longest feather to the point of insertion into the body, and other measures were taken as for the shearwater pair. Recordings were made of their respective Burrow Calls (see Cramp & Simmons 1977; James & Robertson 1985b) from birds calling in burrows, and sonagrams produced as for the shearwaters. Five call variables were measured for comparison between the two species (Fig. 2).

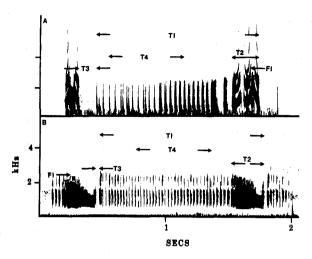


Figure 2. Sonagrams of male (A) Madeiran Storm Petrel and (B) British Storm Petrel showing Burrow Call variables measured: T1 = call length; T2 = breath note length; T3 = gap between successive calls; T4 = rate of note production during 'purr'; F1 = maximum frequency of breath note.

All birds used for the study were known males, sexed either cloacally (Serventy 1956) or vocally (Brooke 1978; James 1984; James & Robertson 1985a, 1985b). Two levels of analyses were undertaken for each pair of species. First, the mensural and call data were compared using univariate analyses of variance (ANOVA); and second, they were compared using multivariate discriminant function analyses. The latter was chosen as a statistical procedure as it is commonly used in biosystematics (Sokal & Rohlf 1969).

RESULTS AND DISCUSSION

Highly significant differences existed between the Manx and Little Shearwaters with regard to their respective body size measures (Table I). In addition, the differences between their respective call variables were also significant (Table I). The multivariate discriminant analyses of the body size and call variables produced highly significant separations for both types of measures (Fig. 3). However, the body size variables produced a stronger discrimination between the two species than the call variables did. A parallel situation existed in the storm petrel pair. Both body size and call variables were significantly different between British and Madeiran Storm Petrels (Table II). In addition, the multivariate discriminant analyses of their respective body size and call variables produced highly significant separations between the two species (Fig. 4). However, as with the shearwater pair, the discrimination was greater using the body size measures.

The results suggest that the quantitative use of call variables alone could be useful in separating petrel taxa as significant separations were achieved (Figs. 3 and 4). Vocalizations have been employed in avian systematics (Löhrl 1963; Lanyon 1969; Selander 1971; Hand 1981; Jouventin 1982; Sparling 1983), yet most studies of the order Procellariiformes have used more traditional morphological methods.

While it may be argued that the comparisons made here were somewhat 'unnecessary' as there are no systematic problems concerning the two pairs of species examined, the analyses were undertaken in order to investigate the relationship between the morphological and vocal approaches. The separations obtained with voice were not as significant as those obtained using body size variables (Figs 3 and 4) suggesting that the use of vocal characters is less reliable than mensural characters. In the present two examples, the interspecific differences in calls more or less parallelled those of morphology. For petrel taxa in which morphological characters were relatively more conservative, however, studies of calls could be important in establishing taxonomic limits, as shown in other groups (Selander 1971).

TABLE I

The mean ± s.d. body size and call variables of male Manx and Little Shearwaters.

Body size n = 36 Manx, 24 Little; call n = 72 Manx, 25 Little.

Variable	Manx	Little	F (ANOVA)	P<
Tarsus (mm)	46.5 ± 0.9	36.8 ± 1.1	1398.5	0.001
Bill (mm)	35.5 ± 1.2	25.3 ± 0.9	1189.6	0.001
Wing (mm)	240.7 ± 4.0	170.8 ± 8.6	1823.7	0.001
Weight (g)	418.2 ± 34.8	160.3 ± 11.9	1218.6	0.001
T1 (sec)	1.4 ± 0.2	1.0 ± 0.1	117.1	0.001
T2 (sec)	0.4 ± 0.07	0.3 ± 0.06	28.1	0.001
T3 (sec)	0.03 ± 0.02	0.02 0.01	5.1	0.05
T4 (sec)	0.1 ± 0.03	0.07 ± 0.03	15.1	0.001
F1 (kHz)	1.3 ± 0.1	2.1 ± 0.2	591.6	0.001
F2 (kHz)	1.2 ± 0.1	$\frac{2.3}{2.3} \pm \frac{0.2}{0.2}$	891.3	0.001

TABLE II

The mean ± s.d. body size and call variables of male British and Madeiran Storm Petrels.

Body size n = 26 British, 34 Madeiran; call n = 30 British, 16 Madeiran.

Variable	British	Madeiran	F (ANOVA)	P<
Tarsus (mm) Bill (mm) Wing (mm) Tail (mm) T1 (sec) T2 (sec) T3 (sec) T4 (n/sec) F1 (kHz)	$\begin{array}{c} 22.6 & \pm & 0.8 \\ 12.0 & \pm & 0.4 \\ 120.4 & \pm & 2.5 \\ 54.2 & \pm & 1.6 \\ 1.4 & \pm & 0.2 \\ 0.3 & \pm & 0.05 \\ 0.02 & \pm & 0.02 \\ 38.3 & \pm & 4.4 \\ 2.2 & \pm & 0.3 \end{array}$	$\begin{array}{c} 23.1 \pm 0.7 \\ 14.7 \pm 0.7 \\ 149.6 \pm 4.0 \\ 65.8 \pm 1.6 \\ 1.8 \pm 0.8 \\ 0.4 \pm 0.09 \\ 0.5 \pm 0.4 \\ 22.3 \pm 3.2 \\ 3.4 \pm 0.3 \end{array}$	5.5 343.1 1038.7 739.2 6.1 18.6 41.9 163.3 144.5	0.05 0.001 0.001 0.001 0.05 0.001 0.001 0.001

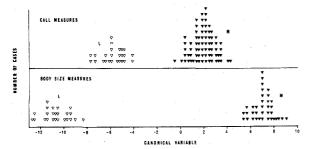


Figure 3. Discriminant analyses of male Little Shearwater (L) and Manx Shearwater (M) call and body size variables. Each point denotes one case.

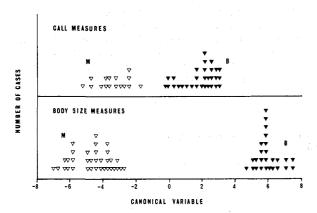


Figure 4. Discriminant analyses of male British Storm Petrel (B) and Madeiran Storm Petrel (M) call and body size variables. Each point denotes one case.

The demonstration of differences between homologous calls alone does not provide unequivocal evidence for the establishment of such limits, but must be used in conjunction with other data in forming a decision.

Vocal characters will probably not gain wide usage in avian systematics simply because they are not needed (Lanyon 1969). Morphological characters have usually been adequate in demonstrating specific limits. In certain groups, however, vocal characters may aid discrimination between taxa e.g., non-passerines that perform courtship under conditions of low light intensity or in habitats that restrict visibility (Lanyon 1969). Systematic studies using voice have been performed on owls (Marshall 1978), and the nocturnal members of the Procellariiformes may also be suitable candidates for similar analyses.

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REFERENCES

AINLEY, D.G. 1980. Geographic variation in Leach's Storm-Petrel. Auk 97: 837-853.

ALEXANDER, W.B. & 14 OTHERS. 1965. The families and genera of the petrels and their names. Ibis 107: 401-405.

BARROWCLOUGH, G.F., CORBIN, K.W. & ZINK, R.M. 1981. Genetic differentiation in the Procellariiformes. Comp. Biochem. Physiol. 69: 629-632.

BOURNE, W.R.P. 1968. Notes on the diving-petrels. Bull. Brit. Orn. Club 88: 77-85.

, & JEHL J.R. 1982. Variation and nomenclature of Leach's Storm-Petrels. Auk 99: 793-797.

BROOKE, M. de L. 1978. Sexual differences in the voice and individual vocal recognition in the Manx Shearwater (*Puffinus puffinus*). Anim. Behav. 26: 622-629.

CRACRAFT, J. 1981. Toward a phylogenetic classification of the Recent birds of the world (Class Aves). Auk 98: 681-714.

CRAMP, S. & SIMMONS, K.E.L. (Eds). 1977. Handbook of

- the birds of Europe, the Middle East and North Africa. vol. 1. Oxford: O.Ú.P.
- DOBZHANSKY, T., AYALA, F.J., STEBBINS, G.L. & VALENTINE, J.W. 1977. Evolution. San Francisco: Freeman Press.
- HALL-GRAGGS, J. & SELLAR, P.J. 1976. Distinguishing characteristics in the burrow-calling of Storm and Leach's Petrels. Brit. Birds 69: 293-297.
- HAND, J.L. 1981. A comparison of vocalizations of Western Gulls (Larus occidentalis occidentalis and L. o. livens). Condor 83: 289-301.
- HARPER, P.C. 1978. The plasma proteins of some albatrosses and petrels as an index of relationship in the Procellariiformes. New Zealand J. Zool. 5: 509-548.
- . 1980. The field identification and distribution of the prions (genus Pachyptila), with particular reference to the identification of storm-cast material. Notornis 27: 235-286.
- IMBER, M.J. 1985. Origins, phylogeny and taxonomy of the
- gadfly petrels *Pterodroma* spp. Ibis 127: 197-229. JAMES, P.C. 1984. Sexual dimorphism in the voice of the British Storm Petrel Hydrobates pelagicus. Ibis 126:
- & ROBERTSON, H.A. 1985a, Sexual dimorphism in the voice of the Little Shearwater Puffinus assimilis. Ibis 127: 388-390.
- -, & -1985b. The calls of male and female Madeiran Storm-Petrels Oceanodroma castro. Auk 102: 391-393.
- . 1985c. The call of Bulwer's Petrel Bulweria bulwerii, and the relationship between intersexual call divergence and aerial calling in the nocturnal Procellariiformes. Auk 102: 878-882.
- JEHL, J.R. 1982. The biology and taxonomy of Townsend's Shearwater. Gerfaut 72: 121-135.
- JOUVENTIN, P. 1982. Visual and vocal signals in penguins, their evolution and adaptive characters. Z. Tierpsychol.,
- Suppl. 24. KURODA, N. 1954. On the classification and phylogeny of the order Tubinares. Tokyo: N. Kuroda.

- LANYON, W.E. 1969. Vocal characters and avian systematics. In Bird Vocalizations, R.A. Hinde (ed.), Cambridge:
- LÖHRL, H. 1963. The use of bird calls to clarify taxonomic relationships, Proc. 13th Intern, Ornithol, Congr. 1962: 544-552.
- MARSHALL, J.T. 1978. Systematics of smaller Asian night birds based on voice. Ornithol. Monogr. 25.
- MATHEWS, G.M. 1948. Systematic notes on petrels. Bull. Brit. Orn. Club 68: 155-170.
- MURPHY, R.C. 1952. The Manx Shearwater, Puffinus puffinus, as a species of world-wide distribution. Am. Mus. Novit. 1586.
 - , & PENNOYER, J.M. 1952. Larger petrels of the genus Pterodroma. Am. Mus. Novit. 1580.
- RISTOW, D. & WINK, M. 1980. Sexual dimorphism of Cory's Shearwater. Il-Merill 21: 9-12.
 SELANDER, R.K. 1971. Systematics and speciation in birds.
- In Avian biology. D. Farner & J.R. King (eds). London: Academic Press.
- SERVENTY, D.L. 1956. A method of sexing petrels in field observations. Emu 56: 213-214. SIBLEY, C.G. & AHLQUIST, J.E. 1972. A comparative study
- of the egg white proteins of non-passerine birds. Peabody Mus. Nat. Hist. Bull. 39.
- . 1983. Phylogeny and classification of birds . & based on the data of DNA-DNA hybridization. In Current Ornithology. R.F. Johnston (ed.). New York: Plenum Press
- SOKAL, R.R. & ROHLF, F.J. 1969. Biometry. San Francisco: Freeman Press.
- SPARLING, D.W. 1977. Sounds of Laysan and Black-footed Albatrosses. Auk 94: 256-269. . 1983. Quantitative analysis of prairie grouse vocaliza-
- tions. Condor 85: 30-42.
- -, & WILLIAMS, J.D. 1978. Multivariate analysis of avian vocalizations. J. Theor. Biol. 74: 83-107.
- THIBAULT, J.C. & HOLYOAK, D.T. 1978. Vocal and olfactory displays in the petrel genera Bulweria and Pterodroma. Ardea 66: 53-56.

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