

MICROGEOGRAPHICAL VARIATION IN THE  
CALL OF THE MALE MANX SHEARWATER  
*PUFFINUS PUFFINUS*  
*LOCALE VARIATIES IN DE ROEP VAN MANNETJES*  
*NOORDSE PIJLSTORMVOGELS*

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*The calls of male Manx Shearwaters at two separate breeding areas on Bardsey Island, Wales were investigated. There was little difference between calls from the two subcolonies when call characteristics were compared separately, but a discriminant analysis placed 75% of the birds into their correct locality. The recent establishment of one of the subcolonies may be responsible for the call variation, rather than any functional explanation.*

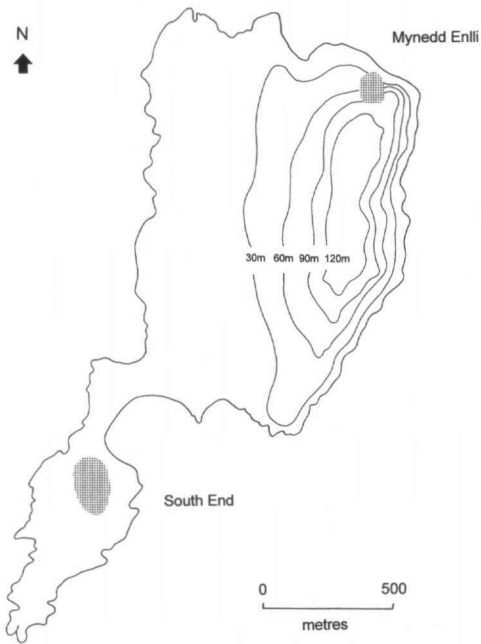
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INTRODUCTION

Compared with work on passerines, patterns of change in seabird calls across geographical areas have received little attention. Where differences have been reported, these have nearly always involved widely separated colonies (Hand 1981; James 1985a; Bretagnolle 1989; Bretagnolle & Lequette 1990; Bretagnolle *et al.* 1991; Tomkins & Milne 1991). The aim of this study was to examine the extent of geographical variation in the calls of male Manx Shearwaters *Puffinus puffinus* on a much smaller scale: between two localities 1.5 km apart on a small offshore island. Manx Shearwaters are nocturnal, colonial burrow-nesters, with a well-developed vocal communication system used for sexual signalling and burrow defence (James 1985b). All male birds can be stimulated to call from nesting burrows by the playback of another male's call, and each male makes an individually distinct variation on a basic, clearly structured, repetitive call pattern (Brooke 1978).

STUDY AREA AND METHODS

The study was carried out on Bardsey, a small island (2.5 km x 1 km) lying 2.5 km from the tip of the Llyn Peninsula, North Wales. The island comprises low-

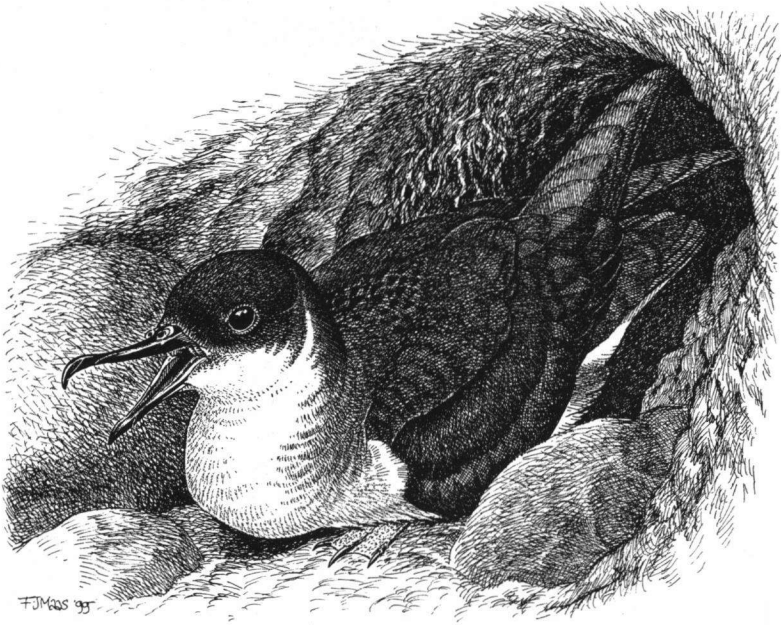


*Figure 1. Bardsey Island, showing the locations of shearwater burrows mentioned in the text.*

*Figuur 1. Bardsey eiland met de plaatsnamen die in de tekst worden genoemd.*

lying agricultural land divided by low drystone walls, and a steep hill (Mynedd Enlli) rising to 170 m in the east (Fig 1). Of 2000-4000 pairs of Manx Shearwaters breeding on the island, about half nest at high density in burrows on the north and east slopes of Mynedd Enlli, the remainder being scattered among field walls across the island (Jones 1988). The South End peninsula holds 400-500 pairs (Smart 1986). Reports from the early part of this century suggest that numbers formerly were much lower and changeable, becoming restricted to Mynedd Enlli and possibly reduced to approximately 30-40 pairs by 1913 (Aplin 1902; Ticehurst 1919; Wilson 1930). This occurred when the human population and agricultural impact on the island were at a maximum; 124 people lived on the island in 1901 (Jones 1988). Therefore, shearwater nesting areas away from Mynedd Enlli are likely to have been established or re-established relatively recently. However, the year when this occurred is not known.

During May 1989, a 'playback' method (James & Robertson 1985) was used to record calls of male Manx Shearwaters occupying breeding burrows at



**Manx Shearwater Noordse Pijlstormvogel (F.J. Maas)**

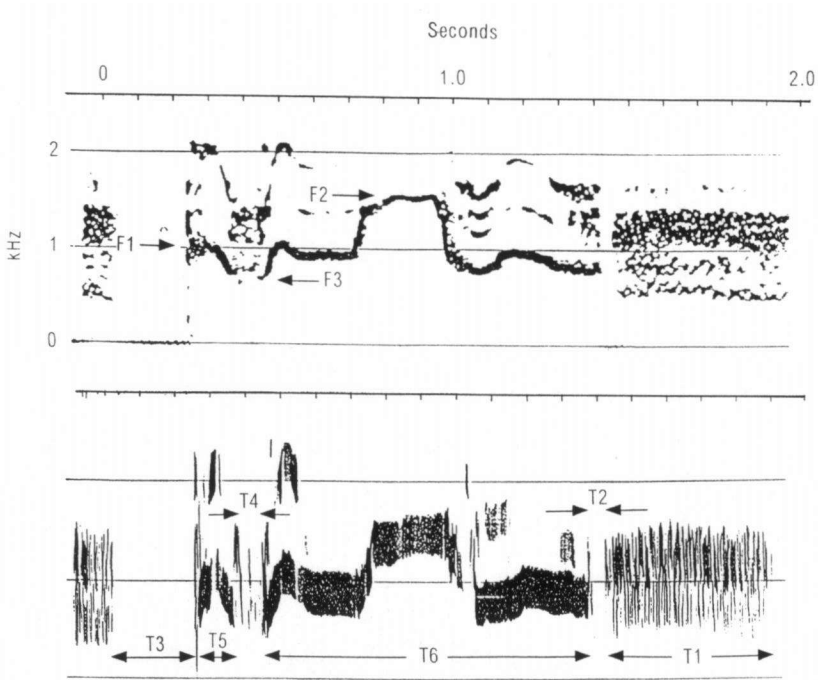


Figure 2. (A) Illustration of three frequency characteristics measured for the call of the male Manx Shearwater: F1 - maximum frequency of first note; F2 - maximum frequency of whole call; F3 - minimum frequency of whole call. (B) Illustration of six temporal characteristics measured for the call of the male Manx Shearwater: T1 - duration of breath intake note; T2 - time gap between breath intake note and rest of call segment; T3 - time gap between successive call segments; T4 - time gap between first note and rest of call segment; T5 - duration of first note; T6 - duration of main part of call segment.

Figuur 2. (A) Illustratie van drie karakteristieke frequenties gemeten bij mannetjes Noordse Pijlstormvogels. F1 = maximale frequentie van de eerste toon, F2 = maximale frequentie van de gehele roep, F3 = minimale frequentie van de gehele roep. (B) zes karakteristieke aspecten van de tijdsduur van onderdelen van de roep. T1 = duur van de toon bij het inademen, T2 = tijdsduur tussen T1 en de rest van het eerste segment van de roep, T3 = tijdsduur tussen opeenvolgende geluidssegmenten, T4 = tijd tussen de eerste toon en de rest van het geluidssegment, T5 = totale duur van het eerste geluidssegment, T6 = duur van het belangrijkste deel van de roep.



Table 2. Discriminant analysis: canonical coefficients (see Fig. 2).

Tabel 2. Discriminant analyse: canonische coëfficiënten (zie Fig. 2).

F1	-0.37	T3	-0.37
F2	-0.25	T4	0.07
F3	0.53	T5	0.45
T1	0.26	T6	0.21
T2	-0.50		

Table 3. Classification summary for discriminant analysis.

Tabel 3. Samenvatting classificatie discriminant analyse.

	number of cases aantal gevallen	correctly predicted correct voorspeld	% corr. predicted correct voersp. (%)
South End zuidzijde	29	23	79%
Mynedd Enlli	28	20	71%
totals totaal	57	43	75%

## RESULTS

Mean values and standard deviations of call characteristics from Bardsey (Table 1) generally conformed with Manx Shearwater calls from other British and Irish islands (James 1985a). Unfortunately a detailed comparison between the two studies is not possible for two reasons. Firstly, different recording equipment was used, which may have given rise to systematic errors (Slater 1991). Secondly, drift in the values of the call characteristics, identified by James (1985a), may have occurred between the dates of the two studies.

On Bardsey, call characteristics, when compared individually, were not very different between Mynedd Enlli and South End. Only one characteristic, the maximum frequency of the first note of the call, resulted in a value of  $t$  associated with  $P < 0.05$ , and as the probability of this occurring by chance in a series of nine  $t$ -tests is quite high ( $P = 0.45$ ), the result is of little consequence. There was no evidence that temporal or frequency characteristics were systematically higher or lower between one area and the other. The discriminant analysis (see canonical coefficients in Table 2) generates a statistic that tests for overall differences between the means, and again, no significant difference between the two areas was found (Wilks' lambda = 0.76,  $F = 1.67$ ,  $df = 9$  and 47, n.s.). However, the same analysis placed 75% of birds into their correct sub-colony (Table 3 and Fig. 3). This is a significantly better classification than would be expected by chance ( $Z = 3.87$ ,  $P < 0.01$ ; Titus *et al.* 1984).

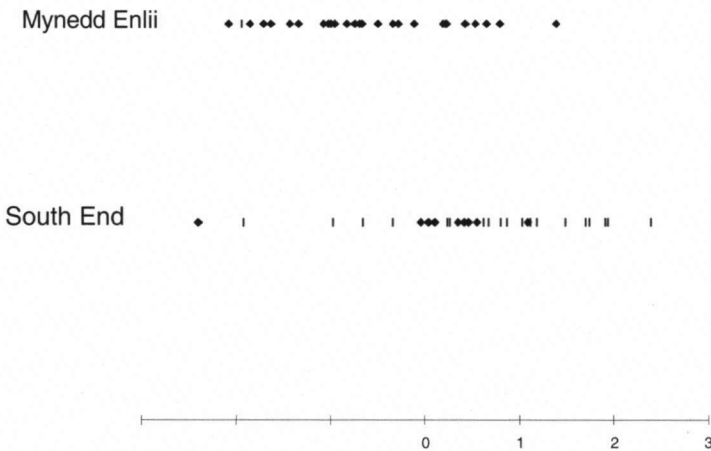


Figure 3. Scatter plot showing the classification of male Manx shearwaters by discriminant analysis of nine call characteristics.

Figuur 3. Puntenwolk op grond waarvan mannetjes Noordse Pijlstormvogels van twee locaties na discriminant analyse van 9 karakteristieken van de roep konden worden geclassificeerd.

## DISCUSSION

Microgeographical differences in bird vocalisations can have several explanations. For example, in passerines it is commonly linked to vocal learning. The pattern of geographical variation is then influenced by the site and extent of vocal learning, and the age at which it occurs (Krebs & Kroodsma 1980; Catchpole 1982). However, there appears to be little if any strong evidence for vocal learning in the Procellariiformes (review in Bretagnolle 1996).

The shearwater calls may be adapted to the local environment. A feature of the two subcolonies sampled in my study is that they occupy rather different habitats. The Mynedd Enlli burrows are densely clumped on a steep, exposed hillside, and were probably dug by the birds themselves, whereas South End birds occupy a set of disused rabbit holes, following the lines of old field walls on level ground. The calls may be subtly adapted to provide optimal acoustic propagation according to the different conditions found at each location; there is evidence for this in some passerines (Morton 1975; Hunter & Krebs 1979). However, the subcolonies studied on Skomer by James (1985a) were also in

contrasting locations, especially with respect to topography and degree of noise from the sea, and there was no noticeable variation in calls between them. This difference in findings between the two studies mitigates against adaptation to local environment being the reason for the observed differences between the two areas on Bardsey.

The call differences could arise if higher quality males nested preferentially in one of the areas, and signalled their status through their calls. Male body weight might be a good measure of the quality of individual petrels, and there is evidence that body weight is correlated with call characteristics in some species (Bretagnolle 1996). However, James (1985a) found no significant correlations between body size and call frequency variables in 22 male Manx Shearwaters.

More generally, shearwaters nesting on Skomer and Bardsey presumably have similar functional requirements for their calls. Therefore, the lack of significant call variation between the Skomer subcolonies suggests that functional explanations in general are unlikely to be responsible for the observed differences between the two areas on Bardsey.

An alternative, non-functional explanation for the pattern on Bardsey, which may also account for the contrasting results between the two islands, is suggested by comparing their histories over approximately the last century. On Bardsey, subcolonies away from Mynedd Enlli appear to have been recently established or re-established. This could have happened in two ways. Firstly, a small subset of the breeding birds on Mynedd Enlli could have moved to the South End, possibly in response to reduced human disturbance at the South End. In this case, divergent calls between Mynedd Enlli and the South End could have arisen by a founder effect, with the strongly developed philopatry normally shown by established breeders in this species providing isolation of birds in the new breeding area; Perrins *et al.* (1973) showed that for Manx Shearwaters ringed on Skokholm when fully grown, 97% of those recaptured had moved less than 45 m. Independent vocal lineages could then develop by genetic inheritance. However, with only an estimated 13-15 shearwater generations having passed between the early years of this century and the late 1980s (Harris 1966), it is unlikely that a few emigrants from Mynedd Enlli could have given rise to the substantial numbers nesting at the South End in 1989. A more likely explanation is that shearwaters from other islands colonised the South End and introduced call variation to Bardsey directly; significant vocal differences between well-separated islands have been detected in this species (James 1985a).

Whatever the cause of the call divergence, we would expect that call differences would rapidly become obscured by those young birds that nest away from their natal burrows at first breeding (estimated at 50% of females and an



unknown proportion of males; Brooke 1990). However, on Bardsey, the short period of time that has passed since the present South End colony was established may not have been long enough to fully eliminate the call differences. In comparison, Skomer's large shearwater colony probably has a long history of stability. This can be inferred because only five or six men were needed to work the Skomer farm in the 1860s, when agricultural activity was at its peak, and even at this time only a small proportion of the land was enclosed (Howells 1968). This suggests that shearwaters over much of Skomer were left relatively undisturbed by human activity. In a stable island population, any original vocal patterning would long since have been lost.

Dialect formation by colonisation, followed by isolation, has been suggested in some songbirds (Baker 1975; Lemon 1975; Baker & Cunningham 1985) and may also occur in petrels (Tomkins & Milne 1991). Corroboration of this mechanism in Manx Shearwaters would require investigation of a colony in the process of establishment and expansion (for example, Storey & Lien 1985).

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#### SAMENVATTING

Roepende mannetjes van de Noordse Pijlstormvogel *Puffinus puffinus* op Bardsey eiland (Wales) werden bestudeerd op twee verschillende plaatsen in de kolonie. Ofschoon er op het eerste gezicht maar weinig verschil bestond in de geluiden die de dieren op beide plaatsen produceerden, bleek na een gedetailleerde studie en een discriminant analyse dat liefst 75% van de vogels op basis van het geluid correct konden worden toegewezen aan één van beide locaties. De recente vestiging van één van beide subkolonies en daarmee het arriveren van allochtone 'pijlstormvogels in het gebied zou kunnen verklaren hoe het verschil in roep tot stand is gekomen.

#### REFERENCES

- Aplin O.V. 1902. The birds of Bardsey, with additional notes on the birds of Lleyn. *Zoologist* 4(6): 8-17, 107-110.
- Baker M.C. 1975. Song dialects and genetic differences in white-crowned sparrows (*Zonotrichia leucophrys*). *Evolution* 29: 226-241.
- Baker M.C. & Cunningham, M.A. 1985. The biology of song dialects. *Behav. Brain Sci.* 8: 85-133.
- Bretagnolle V. 1989. Calls of Wilson's Storm Petrel: Functions, individual and sexual recognitions, and geographic variation. *Behaviour* 111: 98-112.
- Bretagnolle V. 1996. Acoustic communication in a group of non-passerine birds, the petrels. In: Kroodsmas, D.E. & E.H. Miller (eds) *Ecology and evolution of acoustic communication in birds*. Comstock Publishing Associates.

- Bretagnolle V., Carruthers M., Cubitt M., Bioret F. and Cuillandre J.-P. 1991 Six captures of a dark-rumped, fork-tailed storm-petrel in the northeastern Atlantic. *Ibis* 133: 351-356.
- Bretagnolle V. & Lequette B. 1990. Structural variation in the call of the Cory's Shearwater (*Calonectris diomedea*, Aves, Procellariidae). *Ethology* 85: 313-323.
- Brooke M. de L. 1978. Sexual differences in the voice and individual vocal recognition in the Manx Shearwater *Puffinus*. *Anim. Behav.* 26: 622-629.
- Brooke M. de L. 1990. The Manx Shearwater. T. & A.D. Poyser, London.
- Catchpole C.K. 1982. The evolution of bird sounds in relation to mating and spacing behaviour. In: D.E. Kroodsma and E.H. Miller (eds) *Acoustic communication in birds*, 1. Academic Press.
- Hand J.L. 1981. A comparison of vocalizations of Western Gulls *Larus occidentalis occidentalis* and *L. o. livens*. *Condor* 83: 289-301.
- Harris M.P. 1966. Age of return to the colony, age of breeding and adult survival of Manx Shearwaters. *Bird Study* 13: 84-95.
- Howells R. 1968. The sounds between. H.G. Walters (Publishers) Ltd., Tenby.
- Hunter M.L. & Krebs J.R. 1979. Geographical variation in the song of the Great Tit (*Parus major*) in relation to ecological factors. *J. Anim. Ecol.* 48: 759-785.
- James P.C. 1985a. Geographical and temporal variation in the calls of the Manx Shearwater *Puffinus puffinus* and British Storm Petrel *Hydrobates pelagicus*. *J. Zool., Lond. (A)* 207: 331-344.
- James P.C. 1985b. The Vocal Behaviour of the Manx Shearwater *Puffinus puffinus*. *Z. Tierpsychol.* 67: 269-283.
- James P.C. & Robertson, H.A. 1985. The use of playback recordings to detect and census nocturnal burrowing seabirds. *Seabird* 8: 18-20.
- Jones P.H. 1988. The natural history of Bardsey. National Museum of Wales, Cardiff.
- Krebs J.R. & Kroodsma D.E. 1980. Repertoires and geographical variation in bird song. *Adv. Study Behav.* 11: 143-177.
- Lemon R.E. 1975. How birds develop song dialects. *Condor* 77: 385-406.
- Morton E.S. 1975. Ecological sources of selection on avian sounds. *Am. Naturalist* 109: 17-34.
- Perrins C.M., Harris M.P. & Britton C.K. 1973. Survival of Manx Shearwaters *Puffinus puffinus*. *Ibis* 115: 535-548.
- Slater P.J.B. 1991. Learned song variations in British Storm Petrels? *Wilson Bull.* 103: 55-517.
- Smart E. 1986. The use of playback techniques to investigate population and incubation spells in the Manx shearwater. *Report of Bardsey Bird and Field Observatory* 29: 130-137.
- Storey A.E. & Lien J. 1985. Development of the first North American colony of Manx Shearwaters. *Auk* 102: 395-401.
- Ticehurst M.F. 1919. The birds of Bardsey. *Br. Birds* 13: 42-51.
- Titus K., Mosher J.A. & Williams B.K. 1984. Chance-corrected classification for use in discriminant analysis: Ecological applications. *Am. Midl. Nat.* 111: 1-7.
- Tomkins R.J. & Milne, B.J. 1991. Differences among dark-rumped petrel (*Pterodroma phaeopygia*) populations within the Galapagos archipelago. *Notornis* 38: 1-35.
- Wilson W. 1930. Some further notes on the birds of Bardsey Island. *Br. Birds* 24: 121-123.