CALLS OF WILSON'S STORM PETREL: FUNCTIONS, INDIVIDUAL AND SEXUAL RECOGNITIONS, AND GEOGRAPHIC VARIATION

by

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(With 2 Figures)
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Introduction

Most of the burrowing petrels are nocturnal on their breeding colonies, and the vocal activity appears therefore to be of prime importance for reproduction (STOREY, 1984) and pair-establishment (JAMES, 1985). Visual signals are thought to be secondary compared to vocal ones, especially in mate attraction and burrow defence (BROOKE, 1986). Mutual displays are entirely vocal, though a possible use of olfactory signals cannot be rejected (GRUBB, 1974). The functions of mutual displays have been summarized as i) advertisement, ii) synchronization of partners for breeding, and iii) species and sex recognition (HUNT, 1980; JOUVENTIN, 1972). It is presumed that these three functions are to be found the vocal activity of petrels. Another, but underemphasized feature of petrel breeding biology, is individual recognition, which has been tested experimentally (BROOKE, 1978; unpubl. data), and demonstrated by banding programs to be crucial to breeding success (GUILLOTIN & JOUVENTIN, 1980). The aim of this paper is to analyse the calls of Wilson's storm petrel *Oceanites oceanicus*, investigating their functions in advertisement, sexual and individual recognitions. Geographic

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variation in the calls and its possible consequences for species specific recognition are also investigated.

The family Oceanitidae (or Hydrobatidae) comprises the smallest birds of the Order Procellariiformes, with body length ranging from 14 to 26 cm. All the 20 commonly recognised species (HARRISON, 1983) are strictly pelagic marine birds and usually breed on islands. Only two species belong to the genus *Oceanites: O. gracilis* breeds on the Galapagos Islands, and is poorly known (HARRIS, 1969). In contrast, *O. oceanicus*, the Wilson's storm petrel, is widely distributed, and very numerous (several million pairs). Two subspecies are currently recognized, *O. o. oceanicus* breeding north of the Antarctic convergence, and *O. o. exaspeartus*, breeding south of it (BECK & BROWN, 1972). Although many studies have been carried out on its ecology, in the Antarctic (LACAN, 1971), on the Antarctic peninsula (ROBERTS, 1940) and on sub-Antarctic islands (BECK & BROWN, 1972; COPESTAKE & CROXAL, 1985), none of these however have dealt with the behaviour of this abundant species (for example, no sonograms have ever been published). In this paper, I provide a complete repertoire of Wilson's storm petrel vocalizations, followed by the function of each, as tested from the responses of the birds themselves. Individual and sexual recognitions were also investigated, by the analysis of 490 calls from 101 different individuals. Geographic variation in the calls is lastly noted, with tentative explanation for such differences.

Study areas and methods

The Pointe Géologie archipelago lies on the edge of Adélie land on the Antarctic continent, at 66°39′S, and 140°01′E. It constitutes more than 40 islets, only seven of which are large enough to support a breeding population of petrels. At Pointe Géologie, the Wilson's storm petrel breeds usually on slopes, using natural crevices in the rocks as nest chambers. Approximately 2000 pairs breed there (THOMAS, 1986), in dense colonies. Although there is no night in summertime, it is considered to be "nocturnal" in its activities at the colony (BRETAGNOLLE, 1988): birds begin to be active around 18 h local time, and leave the colonies early in the morning from 3 to 7 h. Field work was carried out on Pointe Géologie over a complete breeding season from December 1984 to February 1986. A second study site was used on the Kerguelen islands, situated between 48°27′S and 50°S in cold sub-Antarctic waters. Wilson's storm petrels are distributed in loose colonies throughout the islands, at altitudes below 800 m. Birds are active there during the night, between 22 h and 3 h local time, though first arrivals to the colony may begin at 18 h. Field work was carried out on these islands from November 1987 to February 1988.

Recordings were made using a NAGRA III B tape recorder and a Sennheiser omnidirectional microphone. The birds were often recorded from inside their burrows and sometimes when calling from outside, when the microphone was always less than 0.5 m away from the calling bird. The calls were analysed with a Kay 8800 Sound Spectrographic Display, and sonagrams were obtained using a Kay 6061 B Sound Spectrograph. The physical characteristics taken into account are shown in Fig. 1.

Playback tests were done in the field with a sound amplificator (10W) and two speakers (4W each). In a first set of experiments, the speakers were settled on two small promontaries (50 m apart from each other) in the colony, and all the birds flying or landing in a $2 \times 2 \times 2$ m^3 volume around the speaker were noted. The responses taken into account included: the number of birds flying directly over the speaker ("Direct flight"); the number of birds showing interest by flying in loops over the speaker ("Circle flight"); the number of birds landing ("Landed bird"). Only the two latter responses were considered as positive responses. In a second set, one speaker was placed at the entrance of an occupied burrow, and the sex and type of call made by the responding birds were noted.

Results

1. Description of vocalizations.

Grating call.

This vocalization has previously been described under several names: harsh chattering call (Roberts, 1940), nest advertisement call (Beck & Brown, 1972). Considering its physical characteristics, we prefer to name it grating call, keeping the "chatter" sound for another call. This was the commonest vocalization of the Wilson's storm petrel, and was used by both sexes. It was generally given from inside the burrow, though sometimes a single bird (most frequently a male) would utter it from a promontary, and exceptionally when flying. The grating call is constituted of syllables (Fig. 1) varying in number from three to over 40. Two variants of the call could be distinguished: a short call comprised three to six syllables, and a long one usually eight to 12 syllables but sometimes more. Syllables were very similar one another, whether considering calls of a single bird or of the whole population (Fig. 1).

Chattering call.

Although rather common, this vocalization has not previously been mentioned or considered only as an occasional variant of the grating call (Beck & Brown, 1972). It is constituted of a varying number of syllables but fewer than in the grating call. Unlike the grating call, the chattering call was given only by males. It was uttered preferentially from outside the burrow (from a promontary), though sometimes from within. In the latter case, mates were usually together and the chattering call was given in association with the grating call. It was never heard from a flying bird.

Other calls.

Two uncommon vocalizations complete the vocal repertory of the species; they both consist of repetition of a single syllable (Fig. 1): the peeping call (Roberts, 1940) appeared to be uttered by both sexes, especially when handled by man. In the few instances when it was heard under natural conditions, it was produced by flying or birds on the ground. The second call is structurally similar to the former, but lower in frequency. Rarely uttered, it could be the equivalent of the sparrow-like call described by Roberts (1940) and/or the call given at sea (Murphy, 1936).

Chicks produced only one vocalization, very similar to the peeping call of adults (Fig. 1). The chick call was emitted while a parent is in the burrow, and seemed to play the role of an appeasement contact call. It was possible to induce this call by touching the very young chick.

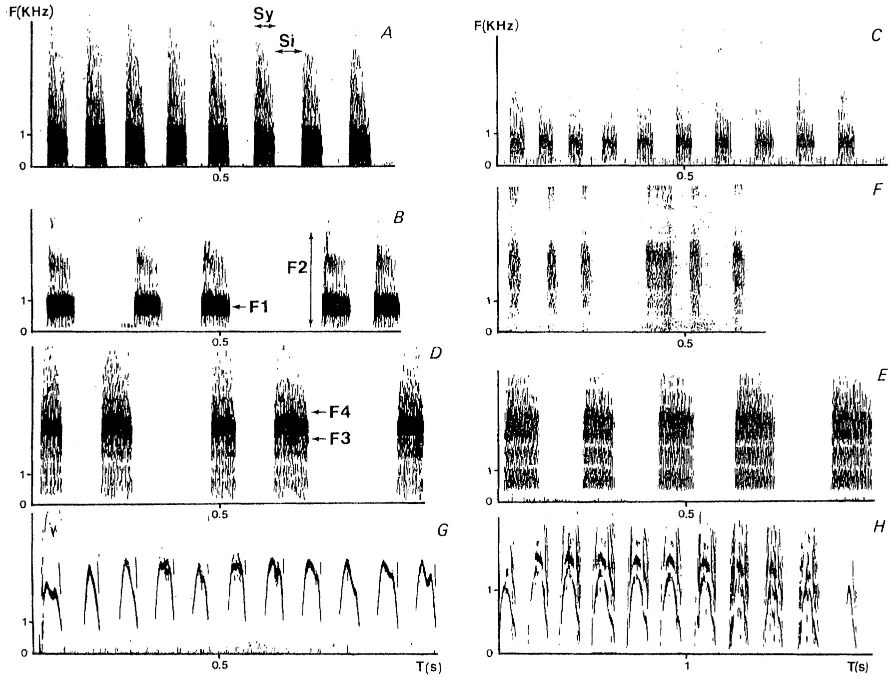

Fig. 1. Sonograms of Wilson's storm petrel vocalizations. Frequency in kHz and time in seconds. Sy and Si denote duration of syllable and silence respectively. F1 to F4 show frequencies used for analyses. A, B and C: chattering calls (A and B from Kerguelen, types B and A respectively (see text); C from Adélie Land). D, E and F: grating calls (D and E: male grating calls from Kerguelen and Adélie Land respectively; F: female grating call). G: chick call. H: peeping call of adult.

2. Experiments and numberings.

Experiments were conducted on the grating and chattering calls made by birds on Pointe Géologie. Table 1 summarizes the results of the first set of experiments with speakers placed on promontaries. The total number of responding birds shows that the chattering call was more attractive than the grating call (Table 1, last column; $t = 4.25$; $P < 0.001$). Significant differences appear between types of response given by birds while grating or chattering calls are played back ($t = 12.7$; $P < 0.0001$ for "circuit flight"; $t = 3.27$; $P < 0.01$ for "landing"). Even chattering and grating calls emitted together are more attractive than the grating call alone ($t = 3.42$; $P < 0.01$), but less than the chattering call alone ($t = 7.71$; $P < 0.001$). Lastly, no significant difference appears when no call or

TABLE 1. Numbers of Wilson's storm petrels responding to the playback of different calls

Played back call	Behavioural responses Direct flight	 Circle flight	 Landed	 Total
Chattering call n = 43	**0.74** (0-4) 1.07	**4.02** (1-6) 1.47	**1.16** (0-4) 1.15	**5.92** 2.69
Grating call n = 43	**1.48** (0-10) 2.23	**0.7** (0-3) 0.88	**0.48** (0-3) 0.73	**2.66** 3.88
Chattering and grating calls n = 20	**0.45** (0-2) 0.76	**1.4** (0-3) 1.14	**0.75** (0-2) 0.63	**2.6** 2.53
No call played back n = 20	**2.05** (1-4) 1.1	**0.3** (0-2) 0.66	**0.2** (0-1) 0.41	**2.55** 2.17

Mean values in bold, range in brackets and standard deviations below. These data were obtained in 20 days of experimentation.

grating call are played back ($t = 1.8$ for "circuit flight"; $t = 0.2$ for "landing").

The direct flight response (first column of Table 1) shows no significant difference for the three types of calls played back. However, chattering call, and chattering and grating calls both show significant differences to the control ($t = 5.35$; $P < 0.001$ and $t = 5.25$; $P < 0.001$). This rather surprising result (as "direct flight" has not been considered as a positive response) simply results from the presence of a "pool" of directly flying birds over the speaker (total of the row "control": 2.55 birds). When the chattering call is played back, some of the birds from the pool fly in circles or land, leaving less birds in "direct flight", and leading to significative differences.

In order to establish the status of attracted birds, storm petrels were mist-netted both while the chattering call was being broadcast and when it was not. Unfortunately, in the storm petrels so far studied, it is not possible to separate the sexes accurately (COPESTAKE *et al.*, 1988; FURNESS & BAILLIE, 1981). Only breeding females could be distinguished from other birds, by cloacal investigation (SERVENTY, 1956). Although fewer breeding females were caught when the chattering call was played back (Table 2), the difference is not significant ($P = 0.2$, Fisher exact test). However, working on the British storm petrel *Hydrobates pelagicus*, FURNESS & BAILLIE (1981) have shown that tape luring (with the purr-call, a highly attractive call) leeds to the capture of more wandering non-breeders than breeding birds. It is not unlikely that the same result should apply to Wilson's storm petrel.

TABLE 2. Status of mist-netted birds when a chattering call is played back or not

	Mist netted birds Breeding females	Males and non-breeding birds	Totals
No call played back	**38** (47.5%)	**42** (52.5%)	**80**
Chattering call played back	**20** (38.5%)	**32** (61.5%)	**52**
Totals	**58**	**74**	**132**

TABLE 3. Frequency of responses by breeding birds to playback of different calls

Call played back	Male response Chattering	Chattering and grating	Grating	No call	Female response Grating	No call	χ^2 Test
Chattering (n = 39)	**0**	**0**	**15**	**8**	**6**	**10**	2.91 NS
Male grating (n = 39)	**0**	**0**	**12**	**7**	**4**	**16**	5.8 $P<0.01$
Female grating (n = 34)	**0**	**0**	**0**	**16**	**4**	**14**	2.17 NS

Differences between male and female responses are tested by χ^2 test.

Both circuit flying and landing were observed in response to the playback of the chattering call. On one night, we caught and banded nine landed birds with colour plastic rings. On the following days, we examined systematically all the accessible nests in the vicinity (within a radius of 25 m around the capture point) and re-discovered five birds. All were males, occupying a burrow less than 5 m away from the capture place. Similarly, we followed six birds in circuit flight over a calling male, and these were all females.

Although the numbers of birds involved in mist netting and these two observations are too small to permit definitive conclusions, they strongly suggest that birds respond differently to the chattering call according to their sex and reproductive status.

The responses of brooding birds to different types of played back calls are given in Table 3. Males only responded with grating calls to played back male calls (both grating and chattering). They also responded dif-

TABLE 4. Frequencies of types of call uttered by males in three different situations

Situation of the bird	Call uttered: Chattering	Chattering and grating	Grating	χ^2 Test
Bird alone (n = 96)	**38**	**35**	**23**	2.85 NS
Flown over by another bird (n = 69)	**33**	**18**	**18**	41.5 P<0.001
Facing another bird (n = 95)	**9**	**16**	**70**	48.7 P<0.001

A χ^2 test compares the results between first and second, second and third, and first and third situation, respectively.

ferently to male and female grating calls, thus indicating an ability to identify the sex of the calling bird ($\chi^2 = 12.7$; $P < 0.001$). Males and females also responded differently to male grating calls ($\chi^2 = 5.8$; $P < 0.01$).

Table 4 compares the types of calls given by males (from outside the burrow) in three situations: when alone, when flown over and when facing another bird. It shows that the grating call was essentially used during face to face interactions, while the chattering call was mainly given when the bird is alone.

Finally in Table 5, frequencies of the two types of male grating calls are compared when the interactions occur either between two males or between a male and a female. The long version was used in agonistic interactions, while the short one served principally in sexual interactions.

3. Sexual differences in calls.

We have shown (Table 3) that birds do recognize the sex of the calling bird. The chattering call, which was only given by males, thus has a potential role in sexual recognition. However, the grating call which was performed by both sexes, had different temporal and frequency characteristics for each sex (Table 6). Female grating calls had a faster tempo and their tone sounded clearer (pers. obs.) and higher than male grating calls (Fig. 1). It seems then that the grating call serves a role in sexual recognition by Wilson's storm petrels.

TABLE 5. Frequencies of types of grating call uttered by males when involved either in Male-Male or in Male-Female interactions

Male-Male interactions (n = 45)		Male-Female interactions (n = 37)		χ^2 Test
Short version	Long version	Short version	Long version	
16 (36%)	**29** (64%)	*33* (89%)	**4** (11%)	3.56 $P<0.05$

TABLE 6. Comparison between male and female grating calls

Physical characters	Male grating call	Female grating call	
Mean F3 n = 38	3.4	3.8	$P<0.01$
Mean F4 n = 20	4.6	5.2	$P<0.001$
First syllable duration	112.8 (n = 23)	77.2 (n = 10)	$P<0.02$
First silence duration	201.8	197.2	NS
Second syllable	108.8	69.8	$P<0.03$
Second silence	228.8	258.5	NS
Third syllable	154.4	160.9	NS
Third silence	177.6	121.8	$P<0.02$
Fourth syllable	146.9	76.26	$P<0.03$
Fourth silence	240.9	262.3	NS

Frequency is given in KiloHertz and temporal parameters are given in miliseconds. See Fig. 1 for F3 and F4 representations. T-test has been used for statistical analysis.

4. Individual variation in calls.

Variation in both calls of the Wilson's storm petrel were compared within and between individuals, under the assumption that individual recognition of calls necessitates individual stereotypy of the calls involved (FALLS, 1982; JONES *et al.*, 1987) *versus* their variation within the population. The coefficient of variation (CV) was then used as a measure of variation and population CV to individual CV ratio as a measure of stereotypy (see JOUVENTIN, 1982, for a similar analysis of penguins calls). Table 7 shows that population variation was not much greater than individual variation in the chattering call (whether considering syntaxic or frequency parameters). A similar homogeneity was found for both sexes when considering frequency parameters of the grating call. The syntaxic parameters of the grating call, however, showed much greater between-, than within- individual variation (for both sexes). The calculation was performed on the seven first syllables, a restriction supported by

TABLE 7. Individual *versus* population variation in chattering and grating calls of the Wilson's storm petrel

Call	Temporal parameters: Individual CV (%)	Temporal parameters: Population CV (%)	Temporal parameters: ratio	Frequency parameters: Individual CV (%)	Frequency parameters: Population CV (%)	Frequency parameters: ratio
Chattering call (male)	T 11.1	25	2.3	F1 8.4	10.4	1.2
	Sy 13.5	28.5	2.1	F2 12.5	28.5	2.3
	Si 23.7	35.6	1.5			
	(16)	(24)		(8)	(8)	
	Mean		**2**	**Mean**		**1.9**
Male grating call	T 3.4	18.8	5.5	F3 7.6	14.6	1.9
	Sy 8.7	21.3	2.5	F4 7.6	9.7	1.3
	Si 8.4	28	3.3			
	(17)	(42)		(7)	(9)	
	Mean		**3.8**	**Mean**		**1.6**
Female grating call	T 3.5	35.4	10.1	F3 11.1	23.2	2.1
	Sy 17.4	52.7	3	F4 9.9	13.7	1.4
	Si 13.8	59	4.3			
	(8)	(16)		(6)	(10)	
	Mean		**5.8**	**Mean**		**1.7**

T = syntaxic parameters; see Fig. 1 for other codes. Numbers in brackets for the number of individuals examined (with at least five calls per individual). CV (ratio of mean to standard deviation × 100) are calculated for each individual (for syntaxic parameters, only the seven first syllables are taken into account), and then, their mean of CV is calculated to representing the individual CV. For population CV, one call (mean values) of each individual is considered.

the observation that stereotypy diminishes greatly after the seventh syllable (Fig. 2). Table 7 shows that neither syllable durations nor silence durations were the most stereotyped variables (although silence duration was less variable than syllable duration), while syntaxic parameters showed the highest stereotypy. Females showed a greater ratio than males (Table 7), but this difference was due only to a greater population variability in females (35.4 as against 18.8), the mean individual variability being equivalent for the two sexes (3.4 and 3.5).

5. Geographic variation of calls.

Table 8 compares the characteristics of male and female chattering and grating calls between Adélie land and Kerguelen island. Silence durations of grating calls differed between the two localities, to a similar degree for both sexes. This result confirms our subjective impression in

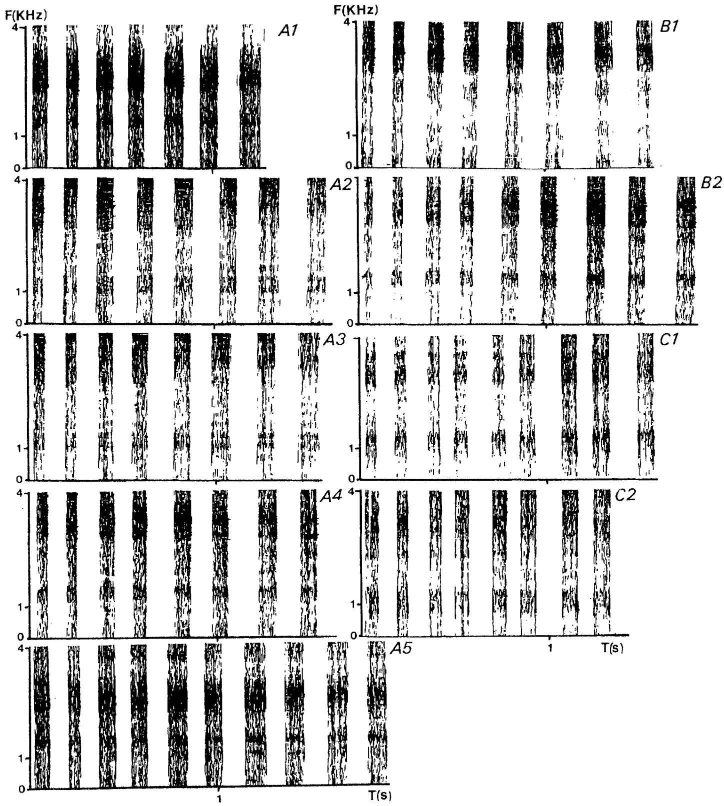

Fig. 2. Sonograms of different grating calls from three males (A, B, and C). Scale is twice that of Fig. 1. Note that stereotypy diminishes after the 6-7th syllable.

the field that the calls of Kerguelen birds had a slower tempo and were higher in frequency than those of Adélie land birds. In contrast, no difference was apparent in the syllable duration of males. On the Kerguelen Island there seemed to be two types of chattering calls (Fig. 1): a first type (Type A) consisted of a long-running chattering call, emitted continuously over several minutes (up to 20 mn), with no distinct interval between successive calls. This type was never heard in Adélie Land. The second type (Type B) was similar to the Adélie Land chattering call. The duration of both syllables and silences were significantly different between the two localities. On the other hand, the number of syllables per call and the frequency parameters did not differ significantly between the two localities.

TABLE 8. Comparison between the calls of Wilson's storm petrel from Adélie land and Kerguelen island (chattering and grating)

Call	Parameter	Adélie land	Kerguelen	Test
Chattering call	N of Sy/call	6.4 (3.6) (55)	5.9 (2.5) (100)	ns
	Sy duration	90.2 (33.5) (10)	119 (28.8) (12)	p<0.01
	Si duration	100.4 (18.6) (10)	141.8 (23.3) (12)	p<0.01
	F1	1.6 (11)	1.63 (13)	ns
	F2	3.2 (11)	2.8 (13)	ns
Male grating call	Sy duration	144.6 (29.8) (23)	155.8 (36.7) (13)	ns
	Si duration	220.4 (34.4) (23)	299 (66) (13)	p<0.01
	F3	3.2 (0.49) (22)	3.7 (0.63) (16)	p<0.05
	F4	4.5 (0.55) (22)	4.9 (0.52) (16)	p<0.05
Female grating call	Sy duration	118.6 (36.7) (9)	78.6 (21.4) (6)	p<0.01
	Si duration	209.3 (39.1) (9)	265.1 (80) (6)	p<0.05
	F3	3.9 (0.56) (11)	3.7 (0.51) (9)	ns
	F4	5.5 (0.31) (11)	4.9 (0.39) (9)	p<0.05

Mean values are given in kiloHertz for frequency parameters and in miliseconds for temporal measurements. Codes as from Fig. 1. First number in brackets represent standard deviation; second number in brackets (lower line) represents sample. A *t*-test or Mann Witney U-test are used for statistical analysis, according to sample size.

Discussion

The discussion will be divided into two parts, dealing with the behavioural functions of the calls, and then with some aspects (causes and consequences) of their geographic variation.

1. Function of calls.

The chattering call is highly attractive to other birds, most likely to non-breeding females (Tables 1, 2 and 4). Thus it appears to be a male sexual advertising call, its function being to attract females to a calling male who owns a nest. Its physical features, a wide frequency range and the repetition of a monosyllable, facilitate locatibility of the emitter (MARLER, 1955; KONISHI, 1973; and WILEY & RICHARDS, 1977 for a review). The chattering call carries no individual information which is comprehensible when regarding its function.

The grating call has two different functions according to the number of syllables it includes. The long version is used in agonistic interactions (Table 5), being uttered mostly in intra-sexual competition during mating. The short version signals sexual identity. As an equivalent of the mutual display of Wilson's storm petrel, the short grating call also has a role in synchronizing partners for breeding (HUNT, 1980). The grating call is highly stereotyped and individualized (Table 7, Fig. 2). Although acoustic individual recognition has not been established directly in this study, we can confidently assume that: i) mates do recognize each other, as shown for other species of petrels by banding programs (GUILLOTIN & JOUVENTIN, 1980 for the snow petrel) and direct experimentation (BROOKE, 1978; unpubl. data for common diving petrel *Pelecanoides urinator*); and ii) visual identification is very unlikely to be sufficient because the birds do not see each other in the extreme darkness of a burrow. Although olfactory cues cannot definitively be rejected, they also seem unlikely in view of the non-evidence of using their sense of smell at the colonies (BANG, 1966; HUTCHINSON & WENZEL, 1980; but see GRUBB, 1974, for an other opinion).

The peeping call seems to be primarily a distress call (FRINGS & JUMBER, 1954), as it is uttered mainly by birds that are being handled. This interpretation is reinforced by similarities between the peeping call and chicks appeasement contact calls.

2. Geographic variation.

Two subspecies are currently recognised in the Wilson's storm petrel (JOUANIN & MOUGIN, 1979). Two birds from the Crozet islands, recorded by P. JOUVENTIN (*O. o. oceanicus*), and four birds from the South Sandwich Islands and five birds from South Georgia, made available by the British Library of Wildlife Sounds (*O. o. exaspeartus*), were well classified by their calls. Geographic variation in vocalizations thus corroborates and parallels the taxonomic conclusions established from morpholical characteristics.

The geographic variation we describe occurs at two different levels: first, the position of the bird uttering the call differed between the two localities. This is well exemplified by the chattering call. On Adélied land, birds can display from outside their burrows in relation of the absence of avian and mammalian predators (LACAN, 1971; pers. obs.). Moreover, daylight is continuous in summertime and birds are then very conspicuous. Thus the sexual advertising function of the call is supported by visual cues. On Kerguelen (as well as on other sub-Antarctic islands) the situation is reversed. Skuas (*Catharacta lönnbergi*) and gulls (*Larus dominicanus*) are active diurnal predators of petrels (BECK & BROWN, 1972; ROBERTS, 1940; pers. obs.). The Wilson's storm petrels therefore display and call from inside their burrows and at night. We suggest they use the type A chattering call (long running version) as a consequence, which facilitates location of the source bird.

The second level of geographic variation is more difficult to explain as it includes differences in the temporal and frequency parameters of calls. Because they are highly isolated, genetic changes would be expected to evolve in each populations through independant mutational processes (MAYR, 1970), which could be the origin of observed differences. Petrel populations are believed to be almost completely enclosed genetically. This is suggested by the absence of band recoveries of fledgings ringed in a locality and found breeding in another one (WEIMERSKIRCH *et al.*, 1985). Between populations, both biotic and abiotic parameters of the environment generally differ strongly, with the result that selective pressures may also differ. Geographic variation is thus expected to occur, and is widely distributed in birds (see for example KROODSMA *et al.*, 1984). However, the changes only affect some of the physical characters. For example, frequency parameters of the chattering call do not exhibit geographic variation (Table 8). We suggest this is due to conter-selective pressures againt deviation of a key signal, namely the one ensuring species recognition. As given by males to attract non-breeding females, we consider the chattering call as a pre-mating isolating mechanism (MAYR, 1970). It must be noted that frequency parameters were shown to be of prime importance in the species-specific recognition of Wilson's storm petrel (BRETAGNOLLE & ROBISSON, unpubl. data).

Summary

The vocalizations of the Wilson's storm petrel (Class Aves) are described briefly. The functions of these calls was determined by experimental playback. The grating call was highly stereotyped individually, and was used in sexual contexts (short version) or agonistic situations (long version). In contrast, the chattering call, displayed only by males, was used for self-advertisement and species recognition. The geographic variation of calls exhibited between two different populations is discussed.

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Résumé

Dans cet article, nous examinions les vocalisations émises par le Petrel de Wilson *Oceanites oceanicus*. Dans un premier temps, nous décrivons le "chattering call", émis uniquement par les mâles, et le "grating call", émis à la fois par les deux sexes. Nous déterminons ensuite le signification de ces signaux par des expériences de repasses, et montrons que le "chattering call" a avant tout une fonction sexuelle (recherche d'un partenaire par les mâles non reproducteurs), alors que le "grating call" est lui avant tout territorial (surtout lorsqu'il est émis sous sa forme longue). Nous nous intéressons ensuite aux mécanismes de reconnaissance (identification): par l'analyse de 490 chants (101 individus), nous montrons que la reconnaissance individuelle est basée sur la temporisation (longueurs des silences et des syllables); la reconnaissance du sexe se fonde à la fois sur les fréquences et la temporisation; enfin, nous étudions la variation géographique des vocalisations et ses possibles conséquences sur la reconnaissance spécifique, et montrons que celle-ci est particulièrement nette sur le "chattering call", bien qu'elle n'affecte toutefois pas les paramètres physiques assurant la reconnaissance spécifique.