

## 9 Acoustic Communication in a Group of Nonpasserine Birds, the Petrels

Vincent Bretagnolle

Animal communication has long been a subject of interest to ethologists (e.g., Tinbergen 1952, 1959), and although the concepts and theories have changed, the study of avian bioacoustics has played a central role in developing the field of animal communication (W. J. Smith 1977, R. Dawkins and Krebs 1978, Zahavi 1979a; reviewed in Krebs 1991). Birds communicate primarily through acoustic means: they use vocalizations and nonvocal sounds in territory establishment and defense, mate attraction, pair-bond maintenance, and parent-offspring relationships (Catchpole 1982, Kroodsma and Miller 1982, Searcy and Andersson 1986, Kroodsma and Byers 1991).

Unfortunately, although bird bioacoustics hold a central place in communication studies, the overwhelming majority of functional studies on bird vocalizations have been on passerines, especially oscines. This pattern is particularly true for the studies concerned with sexual selection, species-specific recognition, and geographic variation (Catchpole 1980, Krebs and Kroodsma 1980, Becker 1982, Mundinger 1982, Kroodsma et al. 1984). Though they comprise nearly half of all bird species, songbirds are not necessarily typical of the class Aves. First, though cultural transmission of vocal characteristics is strongly developed in oscine passerines, it is unknown in the suboscines (approx. 1000 species), and outside the Passeriformes has been reported only in parrots, hummingbirds, and perhaps some other groups (Kroodsma 1982a, Kroodsma and Baylis 1982, Baptista, this volume). Second, passerine vocalizations are frequently interpreted in terms of sexual selection theory because characteristics of male calls affect mate choice (Searcy and Andersson 1986, Lambrechts and Dhondt 1987, Alatalo et al. 1990). Oscines, however, usually have feeding territories, and females may be just as likely to base their choice on the quality of the male's territory as on his vocalizations (Radesäter et al. 1987, Arvidsson and Neergaard 1991). Third, in many oscine species, visual signals also play an important role in advertising behavior, either in territory contests or in female attraction (Searcy 1986), although the relative importance of visual and acoustic cues has seldom been determined (but see Yasukawa 1981b, 1990, Metz and Weatherhead 1991). Fourth, many oscines use the same songs both for territorial defense and for mate attraction and are thus

susceptible to both intra- and intersexual selection pressures (Krebs and Kroodsma 1980; but see Morse 1970, M. S. Ficken and Ficken 1973, R. B. Payne 1979, Radesäter et al. 1987, Radesäter and Jakobsson 1988).

Petrels, which constitute three of the four families of the Procellariiformes, offer an interesting comparison with the passerines, and with research on communication in general. They are a monophyletic taxon with many species (C. G. Sibley et al. 1988, Warham 1990), thus allowing comparative studies, and they feed exclusively on pelagic marine resources and therefore do not hold feeding territories. Though they actively defend their burrows from intruders of their own and other species, males do not guard territories. Female choice, if it occurs, should thus be based primarily on the characteristics of the males or, possibly, of the nest sites. Petrels show delayed sexual maturity (petrels usually breed for the first time at four to six years old: Warham 1990); during the prebreeding period, pair formation always takes several years. Delayed pairing offers the opportunity to study the temporal progression of the pair formation process as well as the possible effects of age and experience on mate choice (e.g., Bretagnolle 1989a). Finally, acoustics are the sole channel used by burrowing petrels for communicating between mates and rivals, a situation that is highly unusual in birds and results from their strictly nocturnal and fossorial habits (Bretagnolle 1990a, MacNeil et al. 1993).

In this chapter I provide the first comprehensive review of what is known about petrel vocalizations, covering all extant genera. I detail both the information content (message) of these vocalizations and their major functions, point out that research techniques must be adapted to this type of bird, and explore how petrel bioacoustics may provide interesting insights into areas of bird communication research.

### Life Histories and Ethology of Petrels

*Systematics.* The order Procellariiformes comprises four families: Diomedidae (albatrosses), Procellariidae (fulmars, gadfly petrels, prions, and shearwaters), Hydrobatidae (storm-petrels), and Pelecanoididae (diving-petrels). Warham (1990) took the term *petrel* to mean any procellariiform, but I follow the more usual restricted sense and exclude albatrosses. The term *burrowing petrels* refers to all petrels except the fulmar group. Petrels represent a significant proportion (approx. 30%) of the world's seabirds, comprising between 90 and 101 species (Jouanin and Mougín 1979, Howard and Moore 1980, C. G. Sibley and Monroe 1990, Warham 1990). The systematics and taxonomy of petrels are still unsettled (Warham 1990); the following information and names are from Warham (1990), except when specified.

*Life histories.* Petrels exhibit extremely diverse ways of life (Jouventin and Mougín 1981, Croxall 1984), ranging from the purely coastal species such as the

diving petrels (*Pelecanoides*) to the strictly pelagic biennial breeders such as the White-headed Petrel (*Pterodroma lessonii*). All species are strictly monogamous, with very high partner fidelity between years (e.g., 93% in Cory's Shearwater, *Calonectris diomedea*; Mougin et al. 1987), and are colonial, though coloniality and fidelity vary according to species. Petrels also show delayed sexual maturity, varying from 2 years (*Pelecanoides*) to 12 (*Macronectes*) years; pair formation takes place during the several years before the birds start to breed.

*Which channel is used for communicating?* Nearly all species of petrels are either strictly or mostly nocturnal on their breeding grounds (Bretagnolle 1990a, Warham 1990, MacNeil et al. 1993). Petrels breed within deep burrows, which further limits their opportunities to see each other, and they strongly avoid moonlit nights (Watanuki 1986, Bretagnolle 1990a). Optical signals are thus totally absent from the communicative behavior of petrels at their colonies, but not at sea, where they are active during daytime (Bretagnolle 1993). The only exceptions are the six strictly diurnal species in the fulmar group, which use both optical and acoustic signals, as do the albatrosses (Luders 1977, Bretagnolle 1988, 1989a). Petrels have well-developed olfaction (Bang 1966), which they use to locate food (review in Verheyden and Jouventin 1994). Whether petrels also use their olfaction for communication is still under debate, but it seems unlikely (Hutchison and Wenzel 1980, Bretagnolle 1990b, unpubl. data; but see Grubb 1974). Colony location and homing were previously attributed to olfactory navigation (Grubb 1974), but more recent evidence is contradictory: according to James (1986), petrels use only visual cues to locate their burrows. Tactile communication has never been investigated but is apparently restricted to mutual preening (Bretagnolle unpubl. data). Therefore, sound is by far the dominant channel for communication in the petrels.

### The Nature and Diversity of Petrel Vocal Repertoires

Petrels rely on sound for communication, so their acoustic repertoires would be expected to include different calls for different contexts of communication. In this section, I review the various types of vocalizations and discuss how petrels' nearly total reliance on acoustic signals may have affected their vocal repertoires.

*Sound recordings and analysis.* I tape-recorded petrel calls during more than 20 field trips between 1984 and 1994. My methods of analysis are described elsewhere (Bretagnolle 1989b, Bretagnolle and Lequette 1990, Richard 1991, Genevois and Bretagnolle 1994). During the years 1984–1994, I studied 45 species of petrels in the field, covering all 23 genera except for *Thalassoica* and *Haloccytena* (sound recordings of these genera and some other species were made available to me by other workers).

*Description of vocal repertoires.* The meaning of repertoires, how they should be studied, and how they should be presented are subjects of some debate (see

Schleidt et al. 1984, E. H. Miller 1988, Hailman and Ficken, this volume). For convenience, I distinguish "major" and "minor" calls: major calls are those used for pairing (including sexual and agonistic contexts), and minor calls are all others. This distinction roughly corresponds to the distinction between song and calls that is often made for passerines (see also Hailman 1989). To minimize bias introduced by the well-known large genera, I summarize our current knowledge of vocal repertoires by genus (Table 9.1). The complete vocal repertoire of Bulwer's Petrel (*Bulweria bulwerii*) is provided as an example (Fig. 9.1; see also Figs. 9.2 and 9.3 for additional examples of calls, and Bretagnolle 1988, 1989b for complete descriptions of vocal repertoires).

Without exception, all petrel genera have one or more minor calls and one or two major calls. These calls include the following six categories.

1. *Food-begging calls* apparently exist in the chicks of all species investigated so far, though little attention has been given to them (but see Brooke 1986, Bretagnolle 1988, 1989b, Bretagnolle and Thibault in press). Typically, food-begging calls are given during feeding events. They have also a submissive connotation, as suggested by the fact that they are often given when the chick is disturbed (e.g., by a human observer), and because similar calls are uttered by the adults of several species in apparently submissive contexts (Bretagnolle 1989b; *Halobaena*: Bretagnolle unpubl. data; *Pachyptila*: A. Tennyson in Marchant and Higgins 1990). Food-begging calls of the chicks are structurally very similar across species. Interestingly, chicks of all species of the fulmar group (no data are available on *Thalassoica* chick calls) have an additional call used exclusively for the purpose of food begging (Bretagnolle 1988, 1990c), a character they share with the albatrosses (Bretagnolle unpubl. data).

2. *Copulation calls* are apparently restricted to the shearwaters and some species of the fulmar group (Bretagnolle and Lequette 1990; Audubon's Shearwater [*Puffinus lherminieri*], *Macronectes*, *Fulmarus*: Bretagnolle unpubl. data). These calls are given during copulation but not before, so they cannot be considered precopulatory behaviors. This pattern differs from that found in most other sea-bird orders, which do have precopulatory displays (Tinbergen 1959, van Tets 1965, J. B. Nelson 1978, Jouventin 1982).

3. *Agonistic calls* are minor calls used in agonistic interactions. They are common in petrels, but are not found in all genera or apparently even in all species within the genera in which they do occur. They are present in several species of the genera *Oceanodroma* (Taoka et al. 1988, 1989b), *Pterodroma* (Grant et al. 1983, Bretagnolle 1995), *Procellaria* (Brooke 1986, Warham 1988a), and *Bulweria* (Fig. 9.1).

4. *Distress calls*, such as the calls birds make when handled, occur primarily in storm petrels (all species so far investigated) and some (possibly all) gadfly petrels. No alarm calls (i.e., calls given toward predators to alert conspecific birds) have so far been discovered in petrels, though an alarm visual display is known for *Macronectes* (Bretagnolle 1988). Warham's (1988a) statement that *Procellaria* has alarm calls is probably incorrect; these calls are more likely to be agonistic calls (cf. Brooke 1986, Bretagnolle unpubl. data).

Table 9.1. The vocal repertoires of petrels

Genus	No. of species	No. of species studied <sup>a</sup>	Food-begging call	Copulation call	Agonistic call	Distress call	Contact call	No. of minor calls	No. of major calls	Visual displays	Sources <sup>b</sup>
<i>Macronectes</i>	2	2	2	1	1	0	0	4	2	Yes	1,2
<i>Fulmarus</i>	2	2	2	1	1	0	1	5	1	Yes	3,4
<i>Thalassoica</i>	1	1	?	?	?	?	1	>1?	1	Yes	4
<i>Daption</i>	1	1	2	0	1	0	1	4	1	Yes	4
<i>Pagodroma</i>	1	1	2	1	1	0	1	5	1	Yes	4,5
FULMARS											
<i>Lugensa</i>	1	1	1?	?	0?	?	0?	>1	1	No	4
<i>Pterodroma</i>	24 <sup>c</sup>	7	1	?	1 (2?)	1	1	>4	2 (3?)	No	4,6-12
<i>Pseudobubveria</i> <sup>e</sup>	4	1	?	?	1?	0	0	>1?	1 (2?)	No	4
GADFLY PETRELS											
PRIONS											
<i>Halobaena</i>	1	1	1	0	0	0	1	2	1	No	13-15
<i>Pachypila</i>	6	5	1	0	0	0	1	2	1	No	4,13,16

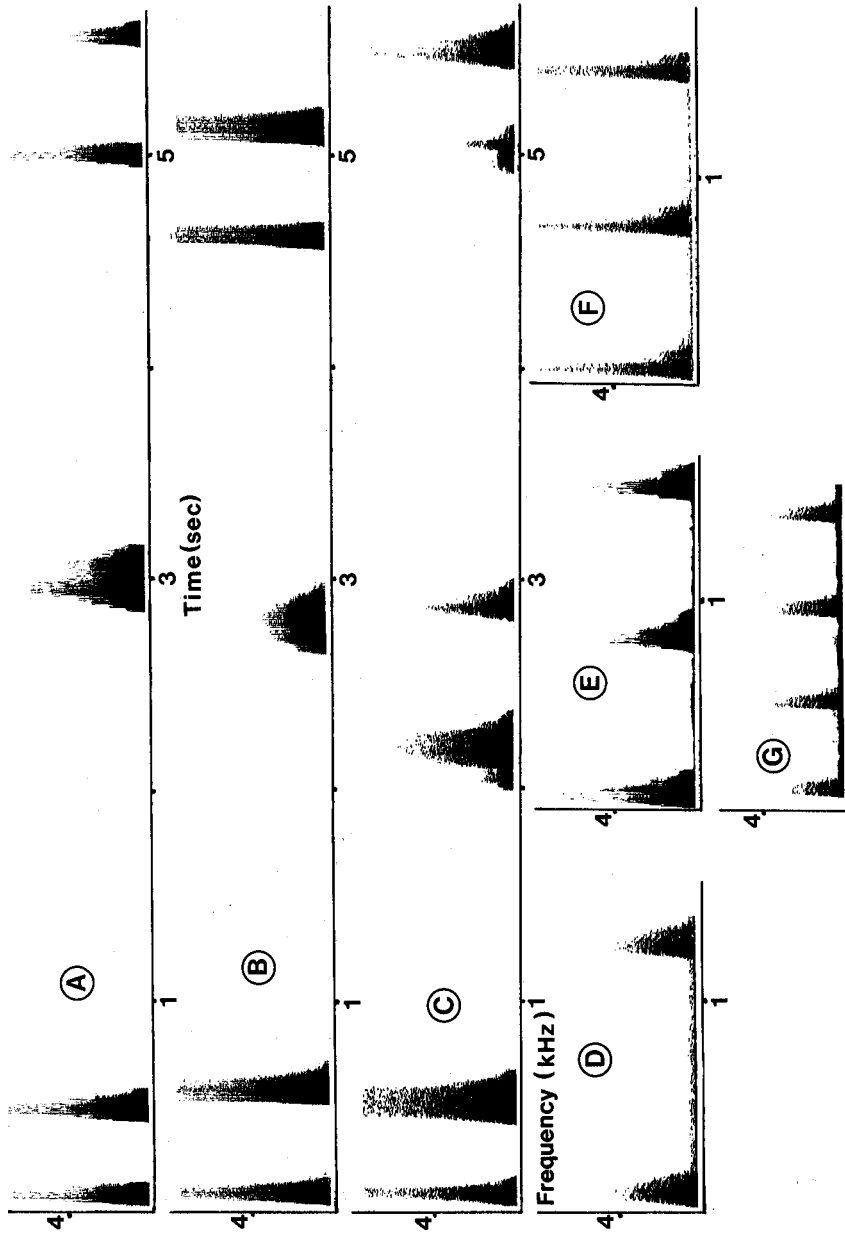
	2	1	1	1	0	1	1	0	0	0	3	2	No
<i>Bubveria</i>	2	1	1	1	0	1	1	0	0	0	3	2	No
<i>Procellaria</i>	4	4	1	1	?	1	0	0	0	>2	2	2	No
<i>Calonectris</i>	2	1	1	1	1	0	0	0	0	2	1	1	No
<i>Puffinus</i>	16 <sup>c</sup>	9	1	1	1	0	0	0	0	2	1	1	No
						STORM-PETRELS							
<i>Oceanites</i>	2	1	1	1	0	0	1	0	0	2	2	2	No
<i>Garrodia</i>	1	1	1	1	?	0	0	0	0	>1?	2	2	No
<i>Pelagodroma</i>	1	1	1	1	?	0	0?	0	0	>1?	2?	2?	No
<i>Fregata</i>	2	1	?	?	?	0	1	0	0	>1?	2	2	No
<i>Nesofregatta</i>	1	1	1	1	?	?	1	?	?	>2?	2?	2?	No
<i>Hydrobates</i>	1	1	1	1	0	0	1	0	0	2	2	2	No
<i>Halocypena</i>	1	1	?	?	?	?	?	?	?	?	?	2	No
<i>Oceanodroma</i>	10 <sup>c</sup>	3	1	1	0	1	0	0	0	2	2	2	No
						DIVING-PETRELS							
<i>Pelecanoides</i>	4	2	1	1	0	0	0	0	0	1	1	1	No

Note: For each genus, the number of call types is given for each category mentioned in the text. Note the differences between genera in the number of major calls.

<sup>a</sup>Including published and unpublished studies.

<sup>b</sup>Sources: 1, Bretagnolle 1988; 2, Bretagnolle 1989a; 3, Luders 1977; 4, Bretagnolle unpubl. data; 5, Guillotin and Jouventin 1980; 6, Grant et al. 1983; 7, Warham 1988b; 8, Warham 1979; 9, Bretagnolle 1995; 10, Bretagnolle and Attié 1991; 11, Tomkins and Milne 1991; 12, Warham et al. 1977; 13, Bretagnolle 1990c; 14, Genevois and Bretagnolle 1994, 1995; 15, Bretagnolle et al. unpubl. ms.; 16, Bretagnolle et al. 1990; 17, James and Robertson 1985a; 18, Brooke 1986; 19, Warham 1988b; 20, Bretagnolle and Lequette 1990; 21, James and Robertson, 1985b; 22, Brooke 1990; 23, Storey 1984; 24, James 1985; 25, Bretagnolle 1989b; 26, James 1983; 27, James 1984; 28, Taoka et al. 1988; 29, Taoka et al. 1989a; 30, Taoka et al. 1989c; 31, James and Robertson 1985c.

<sup>c</sup>Discordant with Warham's (1990) checklist.



**Fig. 9.1.** The vocal repertoire of the Bulwer's Petrel (*Bulweria bulwerii*) contains two major calls (duet call and fast repeat call) and three minor calls (slow repeat call, an agonistic call, and food-begging call and distress call, not shown). Birds were recorded on Salvages Island, in the North Atlantic Ocean, with a Uher 4400 tape recorder and a Sennheiser MD 421 microphone. Sonograms were printed on a Kay Elemetrics 6061B Sonagraph, using narrow-band (45 Hz) and wide-band (300 Hz) filters. (A-C): Three examples of duet calls (A, B, two different males; C, female). (D-F): Three examples of slow repeat call (D, E, two males; F, female). (G) Fast repeat call (female).

5. *Contact calls* are short, repetitive calls given by birds in flight, presumably to avoid collisions. They are known in several genera, particularly *Pterodroma* (Grant et al. 1983, Bretagnolle and Attié 1991, Tomkins and Milne 1991).

6. *Major calls* are given primarily during courtship. Approximately half the genera have a single major call in their vocal repertoires; other genera have two. A typical example of the one-call type is Cory's Shearwater (Bretagnolle and Lequette 1990); Wilson's Storm-Petrel (*Oceanites oceanicus*; Bretagnolle 1989b) is typical of the two-call type. In the repertoires of one-call type species, the single call is always given by both sexes. In contrast, in two-call type species, one type is shared by both sexes, and the other is given either by the male only (e.g., *Oceanites*; Bretagnolle 1989b) or by both sexes (e.g., *Oceanodroma*: Taoka et al. 1988, 1989c; *Bulweria*: Fig. 9.1).

*Acoustic repertoires of petrels compared with those of other birds.* As expected, petrel vocal repertoires include calls that are used in all general contexts of communication: sexual, agonistic, and parent-offspring relations. As petrels have an "obligate" vocal communication system, it might be further predicted that their repertoires have achieved higher levels of diversity than those of other birds. Comparing petrel call diversity (e.g., number, variability in physical structure) with that of other birds is, unfortunately, impossible because complete descriptions of vocal repertoires that cover orders, or even families, are extremely scarce (but see W. J. Smith 1971, Jouventin 1982, Hailman 1989, Hailman and Ficken, this volume). Petrel repertoires typically include six to eight different call types, which certainly does not exceed the usual range of passerine repertoires. In fact, many passerine species have much larger repertoires (see, e.g., Marler 1956, Gompertz 1961, W. J. Smith 1977, Bijnens and Dhondt 1984), apparently because a full range of minor calls is lacking in petrels. Penguins have about as many calls in their repertoire as petrels do (three to six), but they also use optical signals (Jouventin 1982). Gulls, which also use a wide range of optical signals, have more acoustic signals than petrels (Tinbergen 1953, 1959). The only other seabirds that are strictly nocturnal on their colonies are several auklets from the North Pacific, and these also apparently have acoustic repertoires larger than those of petrels (e.g., nine calls in the Ancient Murrelet, *Synthliboramphus antiquus*: Jones et al. 1989). Also, diurnal petrels do not show impoverished acoustic repertoires compared with the burrowing petrels (Table 9.1, Bretagnolle unpubl. data). Thus, there has been no major diversification of calls in burrowing petrels, perhaps because of phylogenetic inertia. As I suggest below, however, subtle variations in major calls can serve to convey a great diversity of information.

#### **Ontogeny and Physical Structure of Calls, and Possible Effects of the Environment**

In the preceding section I pointed out that petrels have several call types in their repertoires. In this section, after establishing that calls are apparently not learned

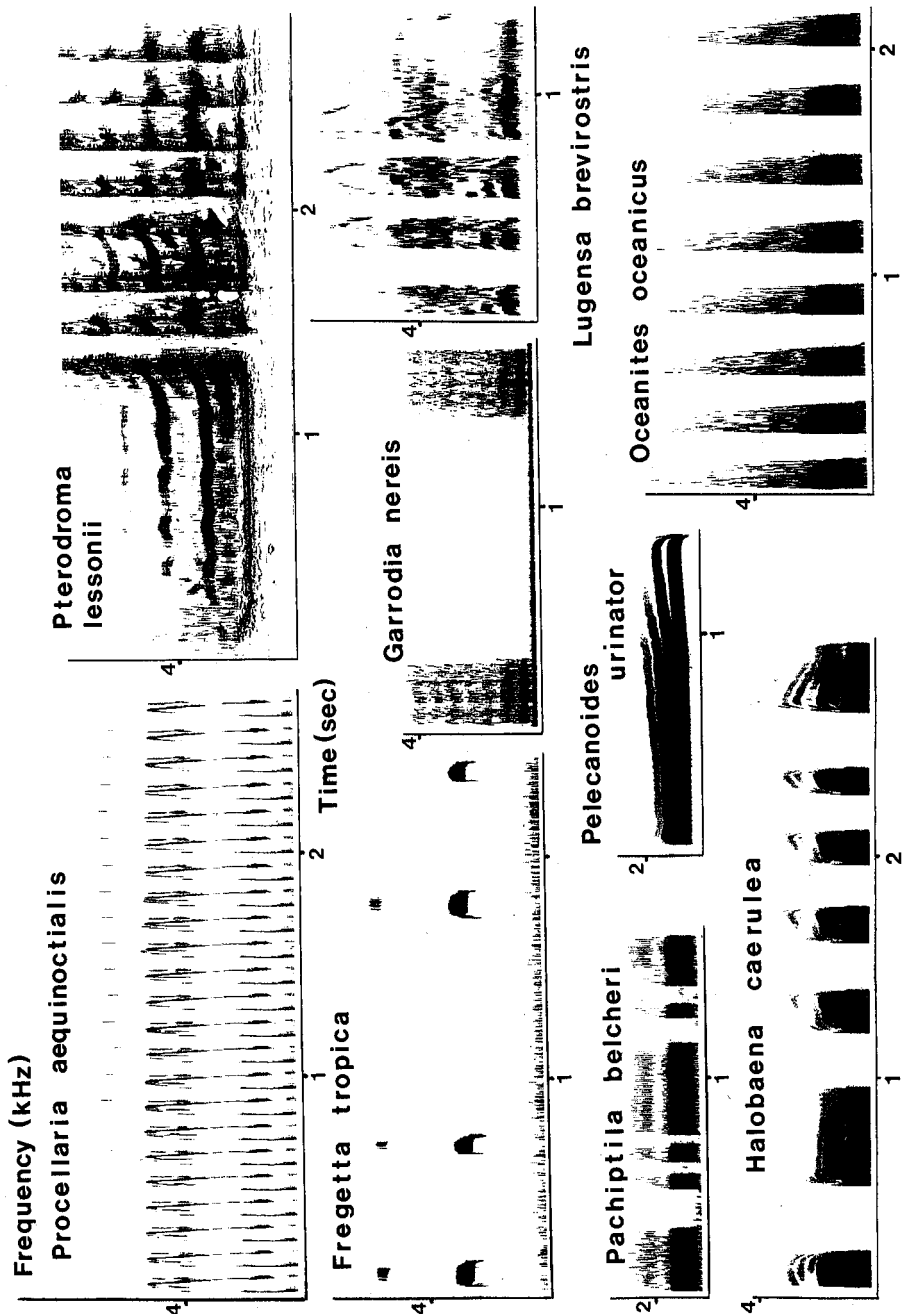


in petrels, I focus on the physical structure of the vocalizations and suggest several factors that may have shaped their diversity.

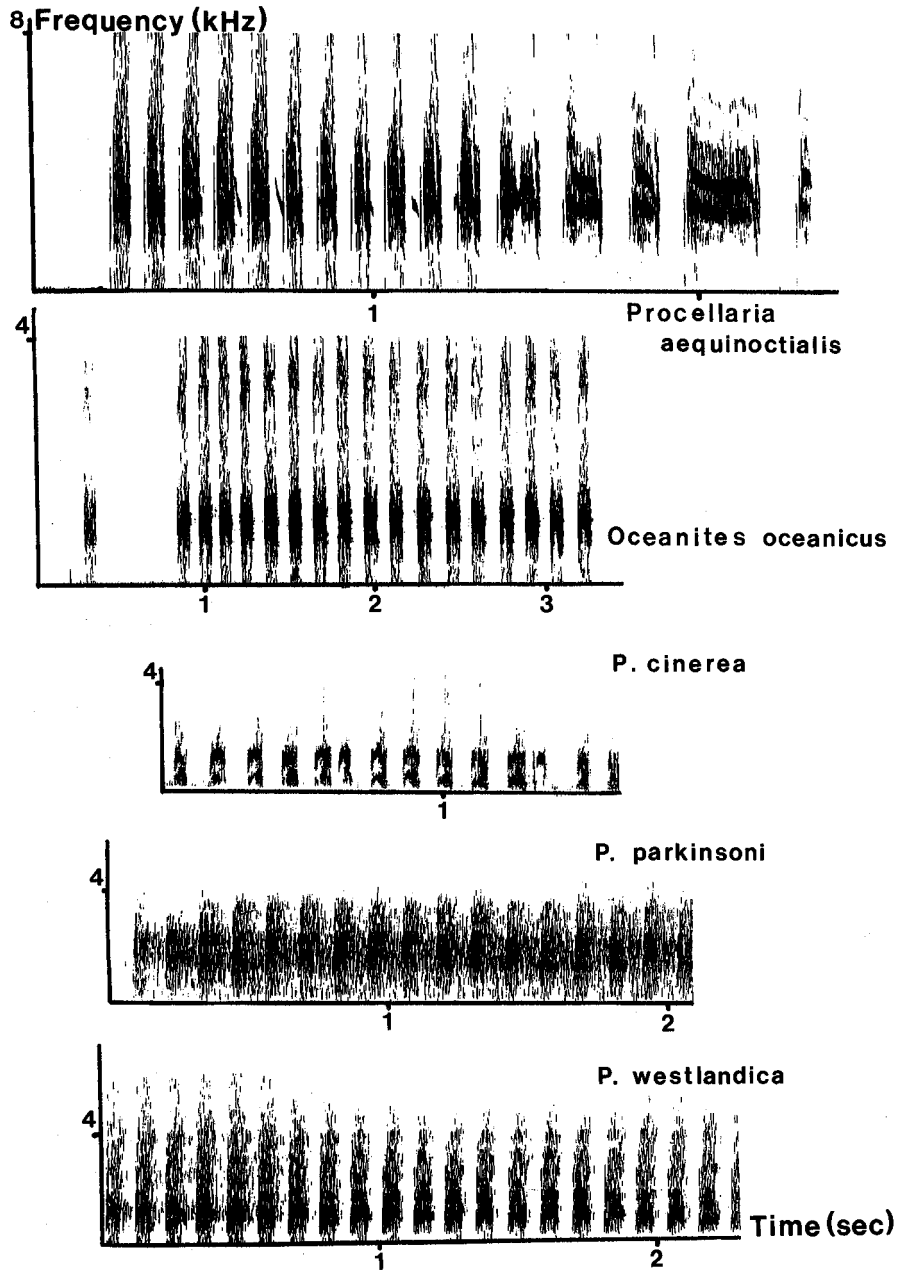
*Ontogeny.* The question of whether petrels learn their calls has not been carefully investigated. Cross-fostering experiments suggest that no vocal learning occurs. In several groups, chicks are able to develop and produce the adult call before fledging (e.g., *Pagodroma*, *Halobaena*, *Macronectes*, *Calonectris diomedea*). In a cross-fostering experiment within the fulmar group, five chicks of the Snow Petrel (*Pagodroma nivea*) reared by Cape Petrels (*Daption capense*) developed the call of their own species (Bretagnolle unpubl. data). James (1985a) claimed that calls of Manx Shearwaters (*Puffinus puffinus*) showed a pattern of change over six years that suggested the calls were culturally transmitted. The change was minor, however, and genetic drift is an alternative explanation. Slater (1991) also questioned James's results and suggested that the use of different tape recorders might explain his observations. Furthermore, penguins, the closest order to the Procellariiformes phylogenetically, do not learn their vocalizations (Jouventin 1982). Thus, no evidence suggests vocal learning by petrels.

*Physical structure.* Sonograms of calls have now been published for approximately 32 petrel species (see Marchant and Higgins 1990, and Table 9.1 for references). In most cases, however, sonograms are not available for the complete repertoire. The physical structure of petrel calls is extremely diverse, with a fundamental frequency and several harmonics (Fig. 9.2). Some species have no detectable harmonics (e.g., *Fregetta* and some *Pterodroma*), but this is rare; others have no clear or detectable fundamental frequency (e.g., *Oceanites*, *Pagodroma*, and some calls of *Procellaria*, *Hydrobates*, and *Oceanodroma*). In the latter cases, the spectral structure of the call can be very complex with rapid frequency and amplitude modulations, and with broad-band noise structures. The calls of several species are apparently made up mainly of noise (Fig. 9.2). Unlike passerine calls, petrel calls lack rapid amplitude modulation (except *Pseudobulweria*: Bretagnolle unpubl. data) and complex and rapid frequency modulation (except some calls of *Procellaria*; Brooke 1986, Warham 1988a). Last, in nearly all species, calls are temporally subdivided into distinct units or syllables (see examples in Figs. 9.2, 9.3). However, *Fregetta*, some *Pelecanoides*, and some *Puffinus* use only one syllable in their calls. Some species use syllables of two or three stereotyped durations (i.e., brief and long syllables); their position within the call may vary between individuals but not within, and this may be a primitive form of syntax (*Halobaena*, *Pachyptila*).

*Two examples of environmental constraints.* Petrels usually breed in huge colonies on small islands, where the sound levels created by the sea and the wind are high. Moreover, petrel colonies are extremely noisy because many birds are calling at the same time (see, e.g., R. H. Wiley 1976, Robisson 1991). Background noise alters signal detection and localization as well as sound propagation. As



**Fig. 9.2.** Sonograms of major calls of some subantarctic species of petrels. Only male calls are represented, and where males have two calls, only the sexual call is shown. Note the distinctiveness of species. Note also that *Pachyptila belcheri* and *Oceanites oceanicus* show some characteristics of broad-band noise. Sonograms were produced on a Kay 6061B Sonagraph with a wide-band analyzing filter (300 Hz).



**Fig. 9.3.** Environmental constraint on petrel calls. Male advertising call of five different species from two genera (*Oceanites oceanicus* and the four *Procellaria* species: *cinerea*, *aequinoctialis*, *parkinsoni*, and *westlandica*). A wide frequency band and repetition of syllables may improve detectability and reduce degradation. Note the structural similarities between *Oceanites* and *Procellaria* in calls, irrespective of phylogeny (the two genera belong to different families), suggesting convergence. Note also that within *Procellaria*, the advertising calls of the male are similar, suggesting phylogenetic inertia.

individuals must be located among the other thousands of birds within the colony, one would expect that the physical structure of the signal would improve detectability and reduce attenuation (R. H. Wiley and Richards 1982, Robisson et al. 1993). Many petrel species have calls with wide spectra (the result of many harmonics or noise) as well as repeated syllables (Fig. 9.3), two acoustic parameters that improve detectability (R. H. Wiley and Richards 1982).

Unfortunately, having highly detectable signals is a risky strategy, because colonial breeding also attracts predators (Bretagnolle in press). In their breeding colonies, petrels suffer from avian predators such as gulls and Brown Skuas (*Catharacta lonnbergi*; Watanuki 1986, Mougeot et al. unpubl. ms.). The latter in particular hunt using acoustic cues provided by their prey (F. Mougeot and V. Bretagnolle unpubl. data). Predation risk is undoubtedly one reason why petrels are nocturnal on their breeding grounds and avoid moonlit nights (Watanuki 1986, Bretagnolle 1990a, MacNeil et al. 1993). To further reduce predation risk, several species perform part of the pairing in flight, hence the existence of aerial calling (see above). But species subject to intense predation might be expected to use signals whose physical structure would further reduce their detectability from predators. The existence of "scrambled" signals in petrels (i.e., the presence of a noise component) and the reduction of the number of syllables might be anti-predator strategies (Figs. 9.2 and 9.3).

### Pair Formation and Sexual Selection

Songs have a dual function in passerines: territorial defense and female choice (e.g., Searcy and Andersson 1986, Falls 1988). These functions are expected of petrel calls, as pair formation relies almost exclusively on calls. As I detail below, playback experiments have actually established both intersexual and intrasexual communication.

*Colony choice and pair formation.* It has been suggested that colonial species use acoustic and optical stimuli to synchronize their breeding activity (following the Darling hypothesis: Darling 1938; review in Gochfeld 1980) or to attract conspecific birds (Wittenberger and Hunt 1985). Two experimental studies provide support for the notion that an assessment of vocal activity is used by petrels in the process of joining a colony (Podolsky and Kress 1989, 1992). The most conclusive evidence comes from general observations; it is well known by birders (especially those who want to catch storm-petrels) that petrels are strongly attracted by conspecific vocalizations, and tape lures have been used extensively to attract petrels to mist nets (Furness and Baillie 1975, Ainley et al. 1976).

All burrowing petrels apparently follow the same pattern in pairing. First, young birds of both sexes visit the colonies, though they may not land, and call actively (see, e.g., James 1985b). Later, immature males try to establish or occupy a burrow; once they get one, they call within it, at its entrance, and possibly in

flight to attract unpaired females (Storey 1984, James 1985b, Bretagnolle and Lequette 1990). In some species, such as the storm-petrels, a specialized call is involved—one of the major calls (Taoka et al. 1988, 1989b, Bretagnolle 1989b). This stage may occur entirely in flight in some gadfly petrels (*Pterodroma*). Then, depending on the species, females who are either in flight (Storey 1984, James 1985b, Bretagnolle 1990c, Bretagnolle and Lequette 1990) or on the ground (Bretagnolle 1989b, Brooke 1986) may engage in courtship duetting with males on the ground. In the last stage, females enter the burrow and duet with the occupant (see, e.g., Bretagnolle et al. unpubl. ms.). In several species, these stages may correspond to different cohorts (birds of successive ages; Serventy 1967, Brooke 1990, Bretagnolle unpubl. data for Blue Petrel). In any case, pair formation takes at least two seasons.

*Playback experiments.* Petrels are nocturnal on their breeding grounds, and they are colonial breeders. For these two reasons the design generally advocated for playback experiments is inappropriate, because it relies on territorial behavior and uses optical signals or movements to score responses (e.g., Emlen 1972, Catchpole 1989, Kroodsma 1989a, c, Searcy 1989). Taking advantage of the peculiar colonial and nocturnal behavior of petrels, researchers have used two different playback techniques to either (1) catch or attract the birds (James 1983, Taoka et al. 1989a, Bretagnolle and Robisson 1991, Podolsky and Kress 1992) or (2) elicit calling as a response (James 1984, Taoka et al. 1988, 1989b, Bretagnolle 1989b, Bretagnolle and Lequette 1990). In the first type of experiment, the relative attractiveness of the different played-back calls is scored by catching or counting the nonbreeders that respond to the loudspeaker by either flying over it or calling. In the second type of playback, birds are subjected to playback tests at their breeding burrows. Brooding birds are silent, and a response is scored when the bird calls in response to the playback.

*Mate attraction and evidence that calls function in intersexual communication.* Very few studies have demonstrated that petrels use calls for mate attraction, and none have documented mate choice via calls (for detailed experimental studies, see Storey 1984, James 1985b, Bretagnolle et al. unpubl. ms.). If petrel calls are to serve intersexual functions, the following predictions should be upheld: (1) there are sexual differences in the calls, (2) sound differences are perceived, (3) male calls are attractive to nonbreeding females, and (4) a selected male trait exists.

Much evidence now supports the first three predictions. Sex differences in petrel voices have been known for a long time (Brooke 1978). The first review discussed 11 species, of which 5 were stated as not showing sex differences (James and Robertson 1985a). Two of those species are in fact sexually dimorphic (Wedge-tailed Shearwater, *Puffinus pacificus*: pers. obs.; and Bulwer's Petrel; Fig. 9.1). In the case of the two *Procellaria* petrels, James and Robertson (1985a)

**Table 9.2.** Individual and sexual signatures in the petrels

Genus	Species	Individual signature (coefficient of variation) <sup>a</sup>	Sexual signature (parameter involved)
<i>Fulmarus</i>	<i>glacialisoides</i>	2.85	
<i>Daption</i>	<i>capense</i>	3.37	
<i>Pagodroma</i>	<i>nivea</i>	1.65	Frequency, tempo
<i>Pterodroma</i>	<i>lessonii</i>	1.57	—
<i>Pterodroma</i>	<i>mollis</i>	4.03	Frequency
<i>Halobaena</i>	<i>caerulea</i>	4.95	Syntax
<i>Pachyptila</i>	<i>desolata</i>	3.92	Syntax
<i>Pachyptila</i>	<i>belcheri</i>	3.03	Syntax
<i>Bulweria</i>	<i>bulwerii</i>	6.77	Frequency, tempo
<i>Calonectris</i>	<i>diomedea</i>	3.82	Frequency
<i>Puffinus</i>	<i>puffinus</i>	1.63	Spectrum
<i>Puffinus</i>	<i>yelkouan</i> <sup>b</sup>	1.16	Spectrum
<i>Oceanites</i>	<i>oceanicus</i>	4.69	Frequency, tempo
<i>Pelagodroma</i>	<i>marina</i>	2.37	—
<i>Fregetta</i>	<i>tropica</i>	1.18	Frequency
<i>Hydrobates</i>	<i>pelagicus</i>	2.46	Spectrum
<i>Oceanodroma</i>	<i>leucorhoa</i>	6.71	Spectrum
<i>Pelecanoides</i>	<i>georgicus</i>	3.98	Spectrum, syntax
<i>Pelecanoides</i>	<i>urinatrix</i>	1.68	Syntax

Notes: Individual signatures are given as an index. Sexual signature indicates the general acoustic variable involved in sex differences (frequency, value of the fundamental frequency; tempo, temporal variables such as rhythm or syllable durations; syntax, number of syllables per call or a difference in the ordination of long and brief syllables; spectrum, a combination of frequency and amplitude variables).

<sup>a</sup>coefficients of variation (Jouventin 1982, Bretagnolle 1989b, Bretagnolle and Lequette 1990)—a large ratio indicates that calls are highly variable between individuals but highly stereotyped within individuals. From Bretagnolle and C. Rabouam (unpubl. data).

cite "Brooke (in prep)" as stating that the species lack sexual dimorphism. But Brooke himself did not write that, because no statistical analysis of sexual dimorphism was in his paper (Brooke 1986). Moreover, Warham suspected sex differences in *P. aequinoctialis* and confirmed them in *P. westlandica* (Warham 1988a). Additional examples not considered by James and Robertson (1985a) are given in Table 9.2. Because sex differences have been detected in most species investigated so far, it is extremely likely that all species do exhibit such differences, although it is more obvious to the human ear in the case of aerial calling species and in burrowing petrels than in diurnal fulmars (James and Robertson 1985a, unpubl. data). Interestingly, sex differences in voice are variably coded on temporal, frequency, or even syntactic parameters according to species (see Table 9.2).

Petrels do perceive sexual differences in voice (James 1985b, Bretagnolle

1989b, Bretagnolle and Lequette 1990, Brooke 1990), and male calls do attract nonbreeders (Furness and Baillie 1975, James 1983, Storey 1984, Fowler et al. 1986, Warham 1988a, Bretagnolle 1989a, Podolsky and Kress 1989, 1992). That male calls attract females especially was suggested for one species and proven for another (Bretagnolle 1989b, Bretagnolle et al. unpubl. ms.).

Finally, the possibility has been investigated that petrel calls convey information about individual quality. Male body weight (or condition) may be a good criterion for female choice in petrels because it is an indicator of fat reserves, which often increase with age and experience (Brooke 1990, Weimerskirch 1992), and because it may be correlated with lifetime reproductive success (e.g., Bryant 1988, Scott 1988). Genevois and Bretagnolle (1994) proved that information on male body weight was conveyed in the calls of the Blue Petrel, because there was a significant positive correlation between body condition and temporal parameters of the call. A similar result has been found for Cory's Shearwater (Bretagnolle and Thibault unpubl. data). It is not known whether the females take this information into account.

*Burrow defense and evidence that calls function in intrasexual communication.* The same type of call can elicit very different responses when played back to nonbreeders (attraction) and breeders (territorial reaction: Bretagnolle and Lequette 1990, Bretagnolle et al. unpubl. ms.). Moreover, in many petrels, birds of a given sex respond only to calls of birds of the same sex (and to their own mates), thus demonstrating the agonistic function of petrel calls (e.g., Taoka et al. 1988, 1989b, Bretagnolle and Lequette 1990, Brooke 1990). Interestingly, female-female competition is strong in petrels, probably as a result of long-term pair-bonding, and females' reaction to female calls is of the same magnitude as males' reaction to male calls (Bretagnolle and Lequette 1990, Bretagnolle et al. unpubl. ms.). Calls apparently contain information relevant to their agonistic content; such "motivational" messages have been found in Wilson's Storm-Petrel (Bretagnolle 1989b). Similarly, Cory's Shearwater, most *Puffinus*, the Blue Petrel, and the prions (*Pachyptila*) increase the modal frequency of their calls in territorial contacts (Bretagnolle and Lequette 1990, Bretagnolle and Genevois unpubl. data).

*Sexual selection.* Calls thus have a function in sexual advertisement and intersexual selection in petrels as well as in intrasexual competition, just as in passerines (see Krebs and Kroodsma 1980, Searcy 1986). But the fact that calls can function in sexual communication does not necessarily mean that sexual selection is occurring (Andersson 1994). Whether differential mating success results from calling differences must be clarified, though petrels, with their very long mating periods, might prove to be difficult subjects. Curiously, two phenomena found in passerines have not been documented in petrels: neighbor recognition (Brooke 1986; Bretagnolle unpubl. data for Blue Petrel) and extra-pair copulations (F. M. Hunter et al. 1992, Swatschek et al. 1994; but see Austin et al. 1993).

### **A Major Constraint on Petrel Calls: Coding and Decoding Messages within a Single Call**

Half the genera of petrels have a single major call in their repertoire that is used both in sexual and agonistic contexts. Below, I discuss how these major calls also encode identifying messages (see W. J. Smith 1977) that identify species, populations, and individuals.

*Evidence for individual recognition.* Individual recognition is common in birds; it has been reported in at least 136 species (Rabouam and Bretagnolle unpubl. ms., Stoddard, this volume). Mate recognition is especially relevant for long-lived and monogamous seabirds because partners usually pair for life, and they breed in colonies (see Beecher 1989). Individual signatures have been widely documented in seabirds (Falls 1982, Jouventin 1982, Rabouam and Bretagnolle unpubl. ms.), though site tenacity can also facilitate mate fidelity (Morse and Kress 1984). Individual signatures occur in at least 19 petrel species (Table 9.2; Brooke 1978, Guillotin and Jouventin 1980, Bretagnolle 1989b, Taoka and Okumura 1989, Bretagnolle and Lequette 1990, Bretagnolle and Rabouam unpubl. data). In all studies to date, individual signatures have been demonstrated for temporal variables but not for frequency or amplitude variables. Investigations of genera that have complex spectra (e.g., *Procellaria*) might lead to different conclusions. Acoustic recognition of the mate has been experimentally established for five species (Brooke 1978, 1986, Taoka and Okumura 1989, Bretagnolle and Lequette 1990; Bretagnolle unpubl. data for Blue Petrel).

*Evidence for species recognition and geographic variation.* Species recognition by voice has been widely documented in birds (review in Becker 1982). In the total absence of optical cues call discrimination and reproductive isolation would be expected to occur between sympatric petrel species—petrel calls should be especially distinct in conditions of sympatry. Petrel calls of sympatric species do differ greatly (Warham 1988a, Bretagnolle et al. 1990, 1991; see also Fig. 9.2). In fact, they are so species specific that they can be used to determine taxonomic relationships (Bretagnolle et al. 1990, Bretagnolle 1995). But character displacement, with calls more distinct in sympatry than in allopatry, has not yet been documented.

Petrels breed on isolated and remote oceanic islands that provide natural geographic isolation; moreover, petrels are highly philopatric (Weimerskirch et al. 1985, Mougouin et al. 1988, Ovenden et al. 1991, Austin et al. 1994). These two characteristics should promote genetic drift, and thus geographic variation. Geographic variation has been detected in petrel morphometrics (Power and Ainley 1986, Massa and Lo Valvo 1986, Bretagnolle et al. 1991, Bretagnolle 1995), coloration (Ainley 1980, Clancey et al. 1981), and genetics (Randi et al. 1989, Ovenden et al. 1991, Austin et al. 1994). Geographic variation is also common in petrel vocalizations and has been found in all families and most genera (James



1985a, Bretagnolle 1989b, Bretagnolle and Lequette 1990, Bretagnolle et al. 1991, Tomkins and Milne 1991, Bretagnolle 1995, Bretagnolle and Genevois unpubl. ms. a, b).

*Coding and decoding different messages within a single vocalization.* Individual recognition requires not only individual consistency but also interindividual variation in the call (Falls 1982, Rabouam and Bretagnolle unpubl. ms.). Species-specific recognition demands that the same call be recognizable to all conspecific individuals. A similar paradox applies for the coding of geographic variation, because population recognition requires within-population consistency (conflicting with interindividual variation) and between-population variation (thus conflicting with species-specific recognition). How, then, can the various messages be encoded together in the call without confusion?

The answer apparently lies in both the coding and the decoding of a message. Detailed analysis of Blue Petrel calls revealed that (1) individual stereotypy and quality are coded on some temporal parameters, especially those at the end of the call (Genevois and Bretagnolle 1994, Bretagnolle and Genevois unpubl. ms. b); (2) geographic variation is coded on both temporal parameters (except those at the beginning of the call) and frequency parameters (Bretagnolle and Genevois unpubl. ms. a); and (3) sexual dimorphism is coded in syntactic parameters (Bretagnolle 1990c). The various messages seem therefore to be coded in different parts of the call or in different parameters. This pattern is also found in Cory's Shearwater (Bretagnolle and Lequette 1990). Further, in this and other species, the meaning (e.g., agonistic vs. sexual) of the same call varies according to the status of the receiver bird (nonbreeder vs. breeder) and its location (flying vs. landed; Storey 1984, James 1985b, Brooke 1990, Bretagnolle et al. unpubl. ms.).

## Conclusions

*The ecology and evolution of vocal signals: phylogenetic inertia and selective pressures.* Petrels are a good model for investigating the evolution of bird vocalizations because the diversity of their acoustic repertoires and the parallel diversity of their life histories suggest a causal link. Below I list five hypotheses that are relevant both to the evolution of petrel calls and to more general evolutionary questions about bird communication.

1. Petrels do not learn their calls. Thus, one may expect to find more divergence between closely related species when they are in sympatry than when in allopatry (see the review in E. H. Miller 1982). Character divergence is not yet documented, perhaps because in sympatry birds are more acute at distinguishing their own species from others (Bretagnolle and Robisson 1991, Bretagnolle unpubl. data).

2. Dialects occur in songbirds as a consequence of song learning, but microgeographic variation also occurs in petrels, even in populations only 2 kilometers

apart (Bretagnolle and Genevois unpubl. ms. a). The origin of geographic variation in petrel calls may be genetic, so petrels might be useful subjects for testing the population marker hypothesis (Nottebohm 1969b, M. C. Baker 1982).

3. Individual recognition probably exists in all petrel species but might be more pronounced in highly colonial species or species showing high mate fidelity.

4. Some petrel species have one major call, others two. Repertoire size (e.g., number of major calls) is not independent of phylogeny (see Table 9.1), but other selective pressures (e.g., reduction of ambiguous signals) might also be present.

5. Some petrel species use aerial calling extensively (e.g., some *Puffinus* and all *Pterodroma*), but others do not. James and Robertson (1985a) and Brooke (1986) discussed aerial calling and suggested relationships between aerial calling and sexual vocal differences. Above, I suggested that predation is an important selective pressure. Curiously, the presence or absence of aerial calling is not consistent within petrel lineages; for instance, species belonging to the same genus can differ greatly (e.g., *Procellaria*: Warham 1988a).

Some of these evolutionary hypotheses are difficult to test because no accepted phylogeny is available at the genus level for Procellariiformes (Bretagnolle 1993). Thus, comparative analyses taking into account the nonindependence of species points cannot be undertaken at present (see Harvey and Pagel 1991). Improved understanding of petrel systematics is a major goal for future research and will, I hope, permit us to distinguish between phylogenetic and environmental effects on the evolution of petrel calls.

### Acknowledgments

I thank all the people who have worked with me: L. Ackerman, V. Barthelemy, E. Buffard, B. Fillon, F. Genevois, F. Mougeot, C. Rabouam, and especially F. Genevois, for our numerous discussions. P. Duncan, S. J. G. Hall, and J. Warham read and improved a first draft of the manuscript and made many corrections on the English. D. E. Kroodsma and E. H. Miller made extensive comments and constructive criticisms that improved the chapter greatly.