

# COMPARATIVE POPULATION BIOLOGY OF FOUR PRIONS (GENUS *PACHYPTILA*) FROM THE INDIAN OCEAN AND CONSEQUENCES FOR THEIR TAXONOMIC STATUS

V. BRETAGNOLLE, R. ZOTIER, AND P. JOUVENTIN

Centre d'Études Biologiques des Animaux Sauvages, C.N.R.S., Villiers en Bois,  
79360 Beauvoir sur Niort, France

**ABSTRACT.**—We studied the morphometrics, breeding biology, genetics, and calls of *Pachyptila desolata*, *P. salvini*, *P. belcheri*, and *P. turtur* in the southern Indian Ocean. Multivariate analysis of the measurements of live birds revealed some overlap among closely related taxa. Comparisons of biological data provided evidence for ecological segregation between taxa, based mainly on phenology of breeding but also on diet. Calls differed significantly between taxa, and multivariate analysis showed no overlap between sympatric taxa. These data were then compared with data from other taxa (*P. crassirostris* and *macgillivrayi*) and from different localities. We support the recognition at the species level of each of the four study taxa. Received 29 June 1989, accepted 6 November 1989.

THE SYSTEMATICS of Procellariiformes, especially at the species level, is unclear (see Bourne 1987). This is partly because related species often overlap in their measurements and color patterns which are the most widely used taxonomic characters in the group. The petrels of the genus *Pachyptila*, the prions, represent a case in point. Prion taxa have usually been divided into two separate groups: the "whale-birds," which comprises *desolata*, *salvini*, *vittata*, and *belcheri*, and the *turtur-crassirostris* group (Fleming 1941, Harper 1980). Between 1930 and 1950, the six taxa were grouped in one to three genera and in four to six species (Mathews 1912, 1938; Murphy 1936; Falla 1940; Fleming 1941), with many subspecies (19 listed in Murphy 1936). The situation was clarified by Falla (1940). Harper (1980) concluded, after an extensive study of both live (at sea) and museum specimens, that Falla's six species were valid. However, Cox (1980) recognized only three species: *vittata* (including *desolata* and *salvini*), *belcheri*, and *turtur* (including *crassirostris*). His argument was influenced chiefly by the extreme geographic variation within each species, the very large overlap in diagnostic characters (measurements and coloration), and the possible existence of hybrids (between *desolata* and *belcheri* on Kerguelen).

One reason for the complexity and contradictions in prion taxonomy may be that most authors have worked on beach-washed and museum specimens (Falla 1940, Cox 1980, Harper 1980). Bill measurements, however, vary widely

in relation to age of specimens (shrinkage of up to 18% for bill width; Kirsky and Harper 1968), age of birds (Richdale 1944, Serventy et al. 1971, Harper 1980), and sample size. As a consequence, some individuals were misclassified or impossible to assign to a particular taxon (Cox 1980). Thus, it appeared that either differences between taxa should be statistically valid (Fulagar 1972, Harper 1980) or the species ranking would have to be abandoned for some taxa (Cox 1980).

Taxonomic problems are now addressed by new methods such as electrophoresis (Avisé and Zink 1988, Zink 1988), DNA-DNA hybridization (Sibley and Ahlquist 1981, Sibley et al. 1988), behavior (Jouventin 1982, Bretagnolle in press a), and ecology (Mayr 1970). According to the Biological Species Concept, closely related species occupy different ecological niches (Mayr 1982). Investigation of ecological niches therefore provides a powerful tool for detecting sibling species (Mayr 1970). None of these methods has been used on prions. Consequently, we compared the population biology of four taxa in the Indian Ocean. We studied morphometrics of live adult birds, analyzed their breeding biology (nesting habitats, phenology, diet, and distribution at sea), and measured allozyme variation and calls. The calls are particularly relevant for nocturnal burrowing petrels, because they may act as isolating mechanisms (Brooke 1986, Bretagnolle in press b). We extend our results to the broader literature to attempt a clarification of prion taxonomic status.

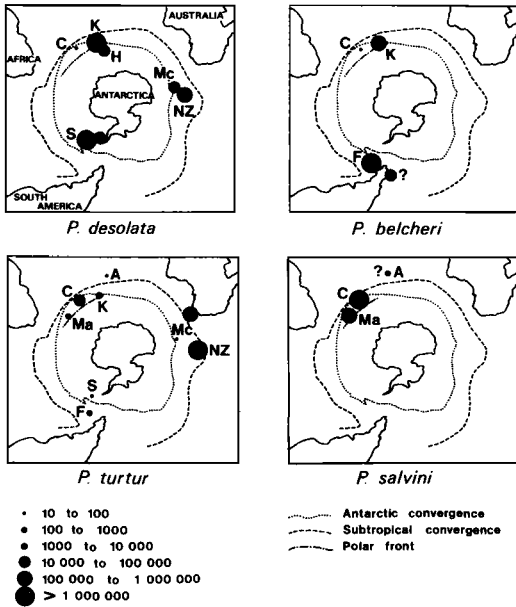


Fig. 1. Distribution of breeding colonies, and numbers of pairs, of four taxa of prions (A = Amsterdam, C = Crozet, F = Falkland, H = Heard, K = Kerguelen, Ma = Marion, Mc = Macquarie, NZ = New Zealand, and S = South Georgia and related islands). Data are from Berruti (1981), Croxall, MacInnes, and Prince (1984), Croxall et al. (1984), Jouventin et al. (1984), Prince and Croxall (1983), Robertson and Bell (1984), Rounsevell and Brothers (1984), Weimerskirch et al. (1989), Williams (1984).

#### MATERIALS AND METHODS

**Localities.**—The study was carried out on the Kerguelen and Crozet archipelagos, and Amsterdam and St. Paul islands. These localities range from 37°S to 49°S, and from 50°E to 70°E in the southern Indian Ocean. They lie in subantarctic and subtropical water masses, respectively (Fig. 1). Each locality is the breeding grounds of two to four different taxa, including cases of sympatry (e.g. *desolata*-*belcheri*) found nowhere else. For details of climate, local topography, and vegetation, see Jouventin et al. (1985), Roux and Martinez (1987), and Weimerskirch et al. (1989).

**Prion taxa.**—The term *taxon* will be used in its restricted sense, that is "a population or a group of populations at any taxonomic level" (Knox and Snow 1987). *Belcheri* and *desolata* breed in vast numbers on Kerguelen (Weimerskirch et al. 1989), and they have bred on Crozet (Despin et al. 1972), although we did not find them there in 1982. *Turtur* breeds at all three localities (St. Paul Island: Tollu 1984). *Salvini* breeds only on Crozet. Two additional taxa will be considered: *macgillivrayi* (endemic to Amsterdam and St. Paul,

and formerly regarded as a subspecies of *vittata* though now linked to *salvini* [Roux et al. 1986]) and *crassirostris*.

**Methods.**—Measurements of 453 live adults included length of exposed culmen, greatest bill width, wing and tarsus lengths, and body mass. *Turtur* and *salvini* were studied on Ile de l'Est and Ile aux Cochons (Crozet), and some of these data have been published (Despin et al. 1972, Derenne and Mougouin 1976, Jouventin et al. 1985, Mougouin 1985). We studied 40 nests of *desolata* and 100 of *belcheri* on Kerguelen (1985–1987). The only notes for *macgillivrayi* are provided by Tollu (1984). Breeding habitats were determined from the relative density of burrow entrances (very abundant, abundant, scarce, or absent) on ca. 400 m<sup>2</sup>. Habitats were divided into four classes (see below). Food samples were collected in January and February from breeders (see Jouventin et al. 1988 for methods). Samples from *turtur* and *salvini* were obtained in 1982 and analyzed by V. Ridoux. Additional samples for *desolata* and *belcheri* were collected during nighttime mist-netting in 1986 and 1987 on Kerguelen. Observations at sea are described in Stahl et al. (1985). Blood samples were analyzed by electrophoresis of blood proteins (see Jouventin and Viot 1985 for techniques). Calls were recorded with a Nagra IV or Uher 4400 tape recorder with a MD 421 Sennheiser microphone. Because petrel calls vary within and between individuals (Brooke 1978, Guillotin and Jouventin 1980), at least 15 calls per individual and, whenever possible, 20 males of each taxon were used for discriminant analysis. *Salvini* was recorded by P. Derenne and J.-L. Mougouin on Crozet in 1975, *desolata* and *belcheri* on Kerguelen in 1987–1988, and *turtur* on Kerguelen in 1984 and Crozet in 1982. *Vittata* was recorded on Codfish Island (New Zealand) during postbreeding visits in April 1986. *Crassirostris* recordings come from published material and New Zealand Television recordings.

#### RESULTS

**Morphometrics.**—Bill width has been claimed to be the best diagnostic character (Fleming 1939) and indeed all pair-wise comparisons between *desolata*, *belcheri*, and *salvini* were significantly different (Table 1; *t*-tests, *P* < 0.01 in all cases). Some overlap occurred (Cox 1980, Weimerskirch et al. 1989). We therefore used a multifactorial analysis which ignored body mass because of its high variability (Table 1). A discriminant analysis on the measurements of *belcheri* and *desolata* classified 98.5% of the birds in their proper categories (*n* = 253). Similarly, 95% of 400 *salvini*, *desolata*, and *belcheri* individuals were classified correctly. The measurements taken from live breeding birds have

TABLE 1. Body mass (g) and measurements (mm) of prion taxa from Indian Ocean islands. Range of variation follows  $\bar{x} \pm \text{SD}$ .

Taxon/locality	n	Body mass	Bill length	Bill width	Tarsus	Wing
<i>macgillivrayi</i> <sup>a</sup>						
Ile St. Paul	11	—	31.1 ± 1.1 29.5–32.5	17.3 ± 1.2 15.7–19.2	36.0 34.0–38.0 <sup>b</sup>	210 ± 5 190–210
<i>salvini</i>						
Ile de l'Est (Crozet)	64	170 ± 11 140–200	30.2 ± 3.7 28.0–35.3	17.2 ± 0.7 15.5–18.6	34.0 ± 1.2 31.2–37.5	195 ± 5 185–205
Ile Cochons (Crozet)	89	159 ± 13 130–210	30.2 ± 1.0 27.5–32.5	16.9 ± 0.8 15.2–18.5	33.8 ± 1.1 31.0–36.8	192 ± 5 184–207
<i>desolata</i>						
Ile de l'Est	3	138 ± 2 —	27.7 ± 1.5 26.0–29.0	13.9 ± 1.3 12.5–15.0	34.2 ± 0.8 35.5–35.0	185 ± 4 182–190
Ile Nuageuses (Kerguelen)	63	145 ± 10 120–169	27.2 ± 1.0 25.0–29.5	14.0 ± 0.5 12.8–15.0	33.5 ± 1.0 31.8–36.3	187 ± 4 178–195
Morbihan (Kerguelen)	118	147 ± 14 115–183	26.9 ± 1.0 24.7–29.5	13.5 ± 0.5 12.1–14.6	34.1 ± 1.2 31.5–37.0	186 ± 4 176–195
<i>belcheri</i>						
Ile de l'Est	4	129 ± 9 115–135	25.3 ± 1.1 24.5–27.0	10.8 ± 0.7 10.2–11.8	34.9 ± 1.4 34.0–37.0	183 ± 4 177–185
Morbihan	66	145 ± 13 118–180	25.3 ± 0.9 23.0–27.3	11.4 ± 0.4 10.2–12.5	33.6 ± 1.1 31.0–36.0	181 ± 4 172–190
<i>turtur</i>						
Ile de l'Est	21	139 ± 17 118–169	22.1 ± 1.1 20.0–24.0	11.1 ± 0.7 10.2–12.8	32.5 ± 1.3 30.0–35.0	178 ± 4 168–186
Ile Cochons	18	132 ± 6 122–148	22.1 ± 1.1 21.0–25.0	11.4 ± 0.9 10.5–12.2	32.7 ± 1.4 30.0–36.0	180 ± 4 170–185
Ile Nuageuses	15	140 ± 20 110–175	22.1 ± 1.2 20.0–25.0	11.5 ± 0.5 10.6–12.5	33.1 ± 0.6 32.0–34.5	181 ± 4 174–189
		<b>Coefficient of Variation<sup>c</sup></b>				
		10%	3.9%	4.3%	3.6%	2.3%

<sup>a</sup> Dried specimen.

<sup>b</sup> n = 30.

<sup>c</sup> Standard deviation divided by the mean.

strong discriminative power even if, as some authors have objected, they cannot classify each individual. In an attempt to generalize from these results, we sought geographic variation at the level of populations with a principal component analysis on 16 populations of the *desolata*, *belcheri*, *salvini*, *vittata*, and *macgillivrayi* group. The results (Fig. 2a) can be summarized as follows: (1) All taxa were clearly separated by the analysis (independently of geographic variation); (2) *macgillivrayi* was placed far from *salvini* and *vittata*, and not between them (axis 2); (3) *desolata* displayed a wide variation within which two groups appeared: one occupied warmer subantarctic islands, and the other colder; (4) the three populations of *salvini* were highly similar to one another. Similarly, 15 pop-

ulations of the group *turtur-crassirostris* were analyzed, using three variables (tarsus length was excluded as data were missing). *Turtur* displayed a large variation, and the two currently recognized subspecies (*turtur* and *subantarctica*; Harper 1980) were not separated completely by the analysis. Further, the three nominal *crassirostris* subspecies overlapped to a large degree with *turtur* (Fig. 2b). Note, however, that sample sizes were small in some cases and specimens were included in the samples.

*Breeding habitats.*—The most abundant petrel on Crozet was *salvini*, which was found in every biotope but favored wet, deep soils under a dense vegetation cover. Deep soils, either wet or dry, were also favored by *desolata*. In contrast, *belcheri* favored stony soils, which may be due

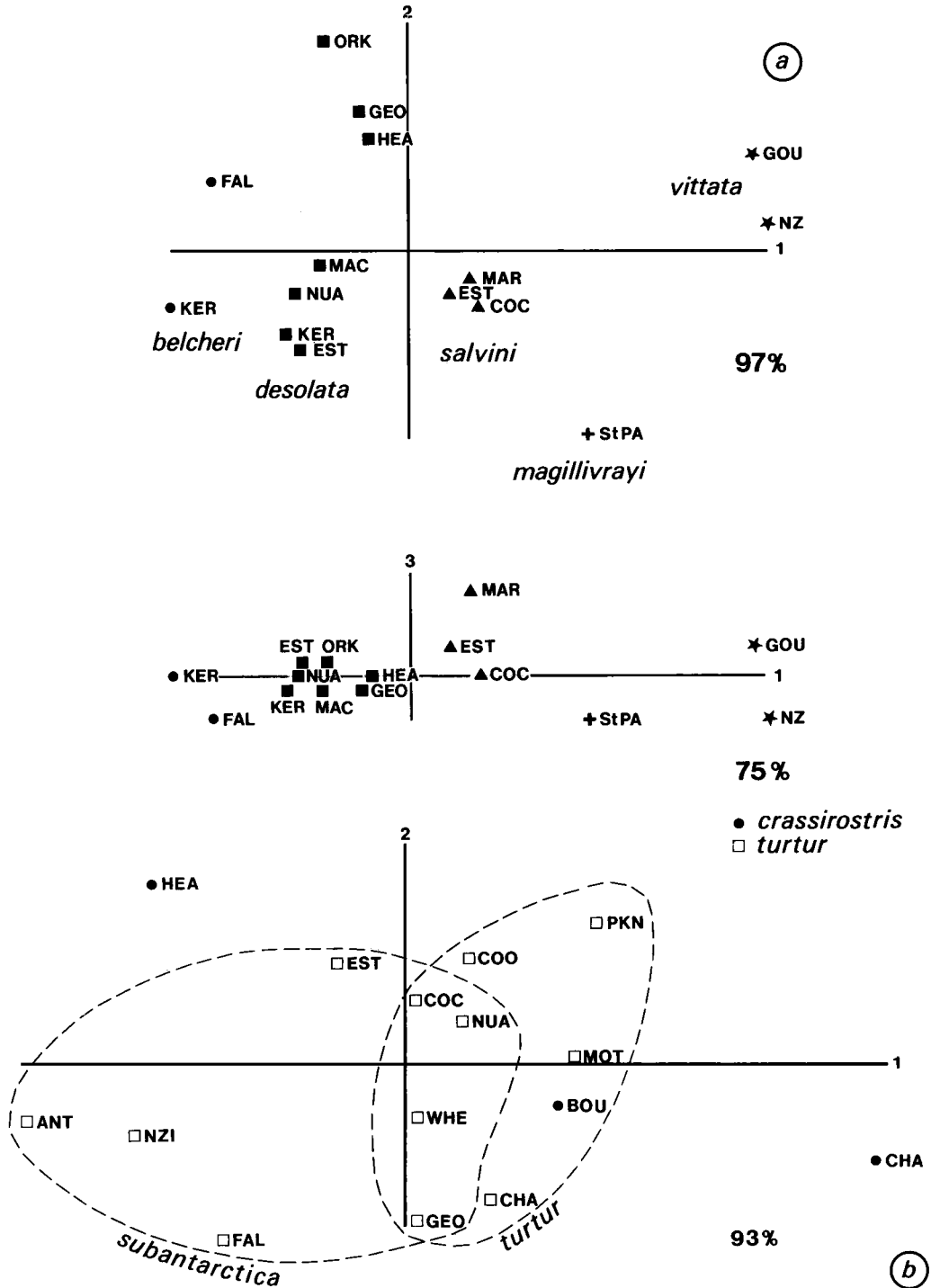


Fig. 2. Principal component analysis on measurements of prions (see text for details). (a) Whale-birds, axes 1 vs. 2 and 1 vs. 3, with percentage of information explained. (b) *turtur-crassirostris*, axes 1 vs. 2, dashed line delimits the two currently recognized subspecies of *turtur*. ORK = South Orkneys, GEO = South Georgia, HEA = Heard, FAL = Falkland, GOU = Gough, NZI = southern islands off New Zealand, WHE = Where,

TABLE 2. Breeding biotopes of four prion taxa in Indian Ocean, in relation to presence of sympatric species and type of soil/vegetation on Ile des Cochons, Ile de l'Est (Crozet), and Îles Nuageuses, Suhm, Chat, Mayes, and Foch (Kerguelen). A dash signifies no petrels; +, ++, +++ are indices of petrel abundance (scarce to very abundant); blank indicates the absence of the biotope on the locality.

Taxon	Sympatric taxon	Locality	Stony soil	Stones and vegetation	Dry and deep soil	Wet and deep soil
<i>macgillivrayi</i>	<i>turtur</i>	St. Paul	++	—	—	—
<i>salvini</i>	<i>turtur</i>	Cochons	+	++	—	+++
	<i>turtur</i>	Est	+	++	—	+++
<i>desolata</i>	— <sup>a</sup>	Possession	++	—	—	—
	<i>belcheri</i>	SW Kerguelen	—	—	++	++
	<i>belcheri</i> + <i>Halobaena</i>	Suhm	—	—	+++	—
	<i>belcheri</i> + <i>Halobaena</i> <sup>b</sup>	Chat	—	++	+++	—
	<i>turtur</i>	Nuageuses	—	+	—	+++
<i>belcheri</i>	—	Foch	—	—	—	+++
	<i>desolata</i>	SW Kerguelen	—	+++	—	—
	<i>desolata</i> + <i>Halobaena</i>	Suhm	++	+	—	—
	<i>desolata</i> + <i>Halobaena</i>	Chat	+	++	—	—
	<i>Halobaena</i>	Mayes	++	+++	+	—
<i>turtur</i>	—	S Kerguelen	+	+++	—	—
	<i>salvini</i>	Cochons	+++	—	—	—
	<i>desolata</i>	Nuageuses	++	—	—	—

<sup>a</sup> Presence of brown rats (*Rattus norvegicus*) at low altitude (i.e. vegetated zone).

<sup>b</sup> Presence of rabbits (*Oryctolagus cuniculus*), which greatly affects vegetation.

in part to sympatry with *desolata*, the Blue Petrel (*Halobaena caerulea*), or both. *Belcheri* dug burrows under vegetation when breeding alone (Table 2). *Turtur* did not dig burrows either on Crozet or Kerguelen (in contrast to New Zealand [Harper 1976]), but used rock crevices. However, the small colony on St. Paul was set in cinder soil, into which *turtur* excavated its burrows.

Each taxon thus used a wide range of breeding biotopes. Preferences emerged only under conditions of sympatry and potential competition.

**Breeding cycle.**—Egg laying was well synchronized and lasted <3 weeks. Clear differences in the laying dates were apparent in situations of sympatry (Fig. 3). For example, *belcheri* and *desolata* were separated on average by 40 days, with no overlap (the last *belcheri* egg was laid 16 days before the first *desolata* egg). Fledging in *macgillivrayi* occurs at least 4 months after *vittata* in New Zealand (Richdale 1944), and 2

weeks after *salvini* on Crozet (Jouventin et al. 1985). There is a well-marked synchrony within *desolata*, *belcheri*, *vittata*, and *salvini* laying and hatching dates, independent of latitude (and sea-surface temperature), although *desolata* from Macquarie (subspecies *alter*) may lay 10 days earlier (Brothers 1986) than other *desolata* populations (Fig. 4). We propose that sympatry does not involve any change in breeding dates. This would indicate that breeding dates are not flexible and potentially may be used as taxonomic characters. Conversely, *turtur* has the widest geographical distribution and shows little synchrony (Fig. 4). Its laying dates appear to vary in relation to sea-surface temperature rather than latitude (southern New Zealand lies in warmer waters than Crozet).

**Diet and distribution at sea.**—We analyzed diets with respect to frequency of occurrence of prey (Fig. 5a). Hyperiid amphipods were found in 77% of samples ( $n = 62$ ). Other crustaceans, such as copepods (found mostly in *salvini*), cirripeds

←

PKN = Poor Knights, COO = Cook Strait, MOT = Motunau, CHA = Chatham, ANT = Antipodes, MAC = Macquarie, MAR = Marion, EST and COC for Île de l'Est and Île aux Cochons (Crozet), NUA and KER for Îles Nuageuses and Kerguelen, and StPA = St. Paul. Data from Berruti and Hunter (1986), Cox (1980), Flemming (1939), Harper (1980), Mougin (1985 and pers. comm.), Richdale (1965), Roux et al. (1986), Strange (1980), Tickell (1962), and Woehler (pers. comm.).

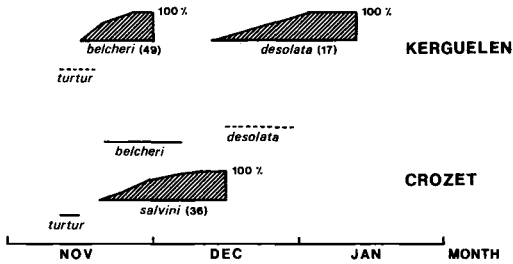


Fig. 3. Dates of egg laying for four prion taxa on Crozet and Kerguelen. When data are detailed, the cumulative percentage is given. When data are scarce, timing is given with dashed line. Sample sizes are in parentheses.

(the main prey of *turtur* on Crozet), and euphausiids—including *Euphausia vallentini* (the only species represented in *belcheri* samples) and *E. superba* (found only in *desolata*)—were each characteristic of only one taxon. Fish were represented substantially by body mass only in *belcheri* samples. Prey preference of taxa overlapped considerably, but the small number of samples analyzed suggested some differentiation. The diets of *salvini* and *turtur* (Fig. 5b) have been analyzed quantitatively to demonstrate that these two taxa feed on different prey.

Distributions at sea do not clearly corroborate the data on diets, largely because of the difficulties of identifying prions at sea. *Turtur* forage mostly over continental slopes (Stahl et al. 1985), whereas *desolata/salvini* (not separated) forage extensively over plateaus and near convergences (Stahl et al. 1985) (*desolata* forages farther south as indicated by the presence of krill in its diet). *Belcheri* are rarely seen near the colonies, but they seem also to favor the high plateaus, where they feed at night (Harper 1972; pers. obs.).

**Genetic data.**—We calculated genetic distances (Nei 1975) for 24 loci on *salvini*, *desolata*, and *belcheri* ( $n = 10$  individuals; Viot unpubl. data). The average distance was 0.077 (0.051 between *desolata* and *belcheri*, 0.067 between *desolata* and *salvini*, and 0.093 between *salvini* and *belcheri*). These distances are relatively low, but not extreme and comparable to other studies (Avisé and Zink 1988). Within the Procellariiformes, the values take an intermediate position between closely related species (0.25 in the two *Pelecanoides* species; 0.08 between the two sooty albatrosses *Phoebastria*), and sibling (0.0008 in the two *Macronectes*; Viot unpubl. data) or

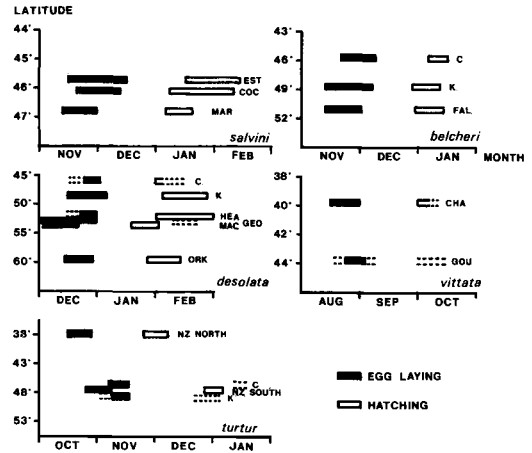


Fig. 4. Comparison of egg-laying and hatching dates for five taxa of prions at breeding localities arranged according to latitude. Codes as in Fig. 1 and Fig. 2. Where data are scarce, timing is shown by dashed line.

subspecies (0.006 for *Calonectris diomedea*; Randi et al. 1989). They are higher than values for conspecific or nonprocellariiform sibling species (Corbin 1983, Avisé and Zink 1988). Electrophoretic data indicate that prions should not be considered sibling species or conspecifics.

**Vocalizations.**—The calls of prions are poorly known (Tickell 1962, Strange 1980). During pair-formation prions typically use a single call (Bretagnolle in press a), which comprises a series of syllables of short and long duration (Fig. 6).

Some physical parameters of calls differed significantly between taxa (Table 3; call duration and modal frequency). In some pairs of taxa, however, physical parameters overlapped (e.g. *belcheri-desolata*), which indicates that a multivariate analysis might be appropriate. A principal component analysis was conducted to find the most discriminant physical characters (out of a sample of 23 temporal and frequency features that describe the call). We performed discriminant analysis on the six taxa, using only the six most discriminant variables (call duration, modal and fundamental frequencies, syllable durations, and number of syllables per call). This analysis classified 85 of 101 males in their proper categories. When only the cases of sympatry were considered (*belcheri-desolata* [ $n = 48$ ], *belcheri-desolata-salvini* [ $n = 68$ ], and *belcheri-desolata-turtur* [ $n = 65$ ]), the discriminant analysis classified every bird in its proper category

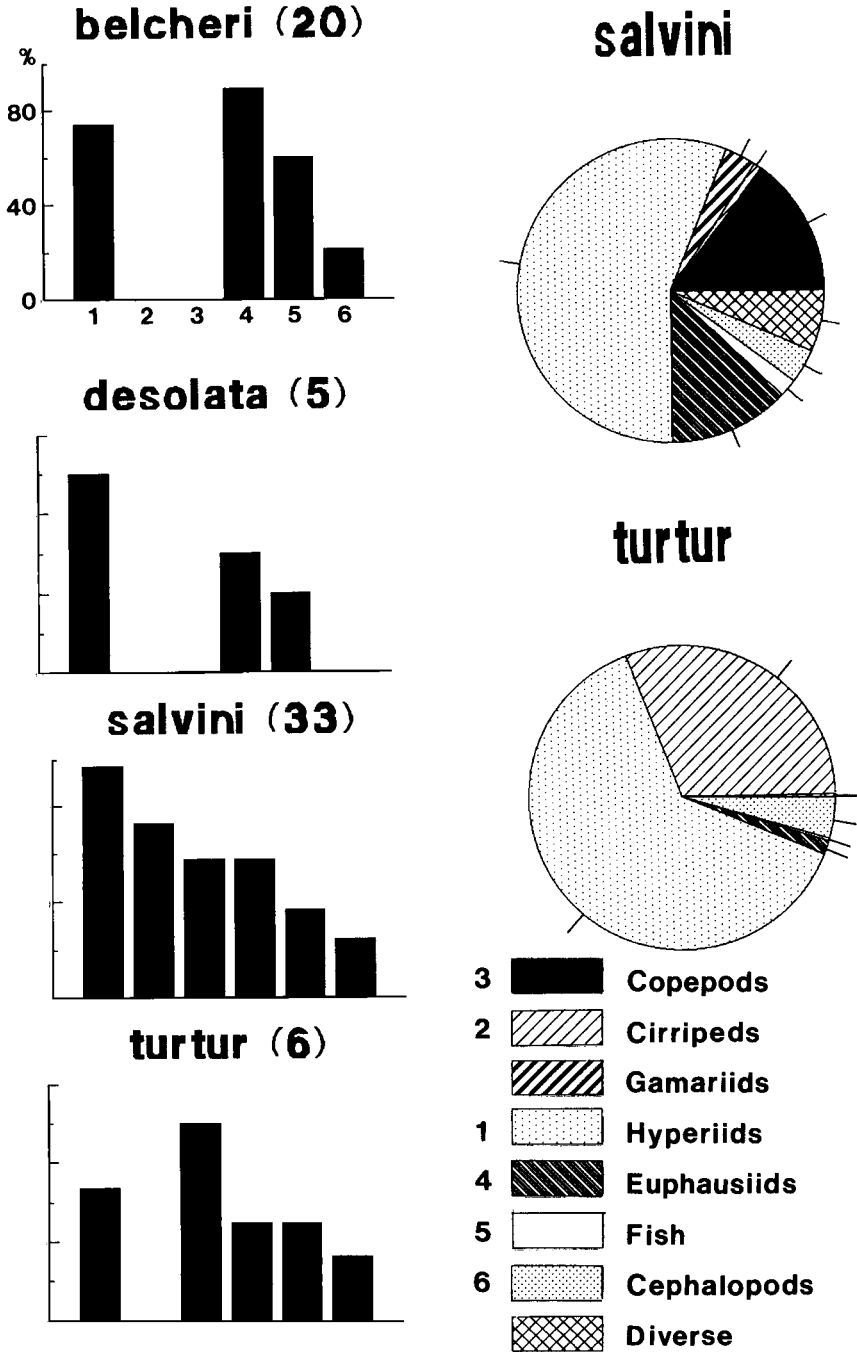


Fig. 5. Diets of four prion taxa (sample sizes in parentheses) from Crozet and Kerguelen. Left: Frequency of occurrence; preys arranged in six classes. Right: Percentages (by weight) of prey items in *salvini* and *turtur* from Crozet (Ridoux, unpubl.).

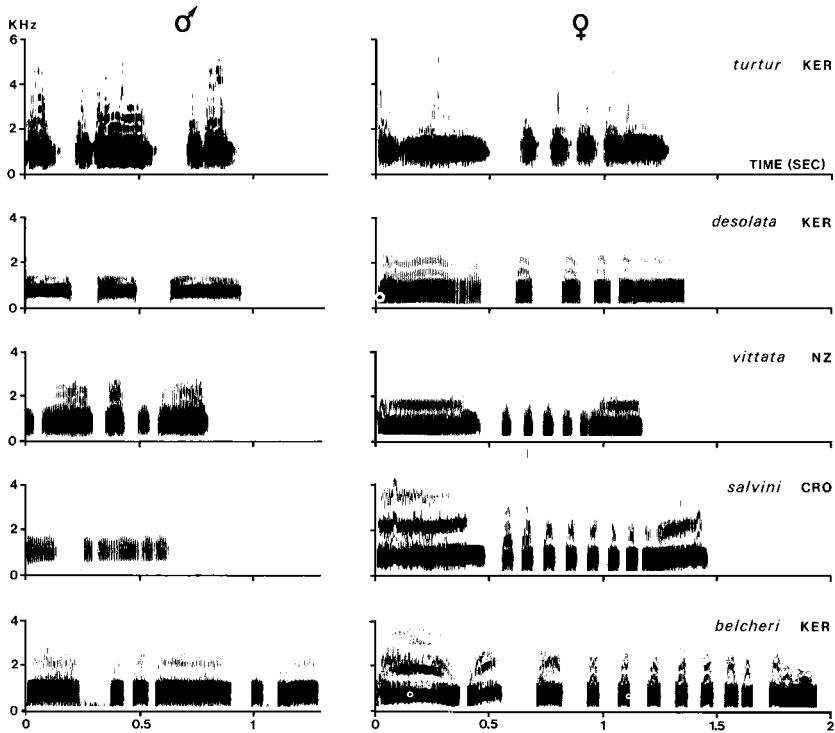


Fig. 6. Sonograms of calls for five taxa of prions. One call illustrated for each taxon and sex. Frequency in kiloHertz, time in seconds, codes as in Fig. 2.

(Fig. 7). Conversely, *salvini* and *vittata*, which do not breed sympatrically, were separated only at 90% ( $n = 32$ ). We analyzed the calls of only five *crassirostris* (from Bounty Island). The calls displayed a large variability and were not obviously different from the calls of *turtur*.

#### DISCUSSION

In his revision, Cox (1980) recognized only two species among the so-called whale-birds: the complex *vittata-desolata-salvini*, and *belcheri*, which was of uncertain status in view of hybridization on Kerguelen. Harper (1980) recognized all four taxa at the species level, although he used the same morphometric criteria. These authors also differed in their interpretation of *turtur* and *crassirostris*.

*Desolata-belcheri*.—These two taxa breed sympatrically in high numbers on Kerguelen (Fig. 1) and provide a natural experiment on breeding isolation. Significant morphological differences existed between the two, although some overlap occurred (Table 1, Fig. 2). They also showed ecological differences in breeding hab-

itat (Table 2), their diets diverged, and their breeding phenology (Fig. 3) showed a separation of >2 weeks in egg laying. Moreover, the date of egg laying was constant among different populations of each taxa throughout the subantarctic area (Fig. 4). Finally, their calls were clearly separated (Fig. 7), which suggests that this may prevent hybridization, because the calls may act as pre-mating isolating mechanisms (Dobzhansky 1937). The differences in morphology, ecology, and behavior lead us to conclude that *desolata* and *belcheri* are closely related but distinct taxa, which should be ranked at the species level because reproductive isolation is achieved on Kerguelen. Cox (1980) thought he could identify hybrids between these species from specimens collected on Kerguelen. We neither saw nor caught such birds, and Falla has relabeled his "Type B" *desolata* (formerly thought to be hybrid) as *belcheri* in 1940 (J. A. Bartle pers. comm.). Hybridization, if it has ever existed, remains to be proved. In any case, it does not invalidate the recognition of the species.

*Vittata-salvini*.—These two taxa do not breed



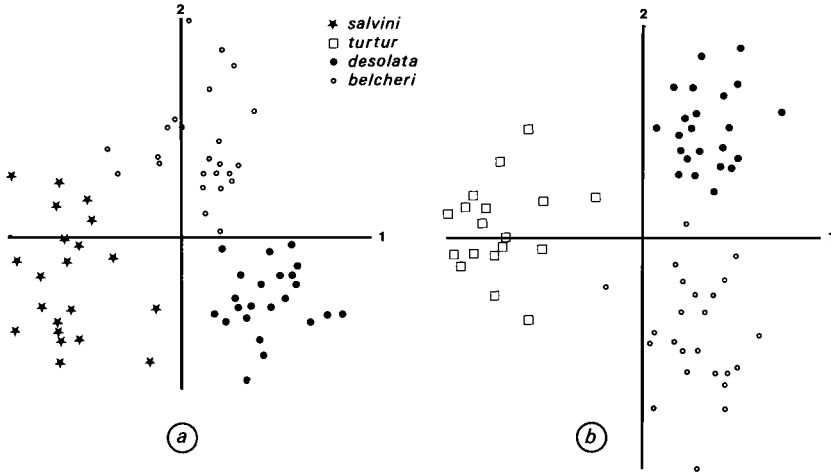


Fig. 7. Discriminant analysis of the calls of four taxa of prions (three breeding in sympatry in each analysis). Each plot represents a bird (average of 15 calls). See text for details.

sympatrically anywhere, and reproductive isolation cannot be observed naturally. The non-dimensional Biological Species Concept (which corresponds to the case of sympatry) must therefore be extended to a multidimensional one (corresponding to allopatry) in which reproductive isolation can only be inferred (Mayr 1982, McKittrick and Zink 1988). Morphological (including bill color), ecological, and behavioral data indicated that two distinct taxa exist, but rank is unclear. In the morphological discriminant analysis (Fig. 2), the distance between the two taxa was much greater than the distance between *belcheri* and *desolata*. This suggests that *vittata* and *salvini* are well separated morphologically and, presumably, genetically. Their calls are different (Table 3, Fig. 7), which suggests that reproductive isolation could theoret-

ically be achieved. Phenology of breeding in both taxa did not vary with latitude (Fig. 4). We conclude that *vittata* and *salvini* constitute separate populations that exploit different ecological niches and should be ranked at the species level.

*Desolata-salvini*.—Although they breed in sympatry on Crozet, the numbers of *desolata* were too small to be considered biologically relevant. It should be noted that *desolata* and *belcheri* were located in a mixed colony in which no *salvini* were breeding (Despin et al. 1972). Nevertheless, the two taxa had different calls (no overlap; Fig. 7). Together with the differences in their phenology, morphology (Fig. 2), and genetics, we conclude that these taxa definitely constitute two distinct species.

*Macgillivrayi*.—This taxon deserves special

TABLE 3. Physical characteristics ( $\bar{x} \pm SD$ ) of prion calls. F1 = Modal frequency; F2 = Following harmonic. Syl. 1 and Syl. 2 represent the mean number of syllables/call with durations between 0.2-0.4 and 0.4-0.6, respectively. Taxon *crassirostris* is not considered in view of insufficient data. \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ; NS = not significant.

Taxon	n	Call length (s)	Syl./call	F1 (kHz)	F2 (kHz)	Syl. 1	Syl. 2
<i>belcheri</i>	27	1.17 ± 0.14	5.7 ± 0.8	0.82 ± 0.07	1.24 ± 0.16	0.9	1.5
<i>desolata</i>	24	1.22 ± 0.14	4.9 ± 1	0.71 ± 0.05	1.05 ± 0.09	0.2	1.1
<i>salvini</i>	17	0.75 ± 0.14	4.3 ± 0.8	0.82 ± 0.09	1.34 ± 0.12	0.9	0.6
<i>vittata</i>	14	0.75 ± 0.11	4.6 ± 0.8	0.75 ± 0.11	1.21 ± 0.17	1.1	0.8
<i>turtur</i>	19	0.66 ± 0.17	3.2 ± 0.4	0.85 ± 0.09	1.37 ± 0.16	0	0.3
<b>t-tests* between taxa</b>							
<i>belcheri-desolata</i>		NS	**	***	***	—	—
<i>desolata-salvini</i>		***	*	***	***	—	—
<i>salvini-vittata</i>		NS	NS	NS	*	—	—

\* t-tests for temporal and frequency parameters.

comments in view of the recent debate concerning its affinities. It has been considered as a subspecies of *vittata* (Harper 1980), and as a subspecies of *salvini* (Roux et al. 1986), the latter because of the blue color of the bill (*vittata* is thus the only taxon with a black bill), bill measurements more like *salvini* than *vittata*, and similarity of breeding dates. As we did not measure or record the calls of the live birds, or take precise breeding data, we are not in a position to infer a taxonomic ranking for *macgillivrayi*. Based on skin measurements, its intermediate position between *salvini* and *vittata* on only some of the characters (Fig. 2) indicates that it may equally be considered as a species.

We agree with Harper (1980), and recognize *belcheri*, *salvini*, *vittata*, and *desolata* as full species. Our morphometric analysis indicates that two, rather than zero (Harper 1980) or three (Tickell 1962), subspecies should be kept for *desolata*. Lastly, it is not clear whether *turtur* and *crassirostris* are different species, although situations of sympatry are known. More data are required on the biology and calls of *crassirostris*.

#### ACKNOWLEDGMENTS

We thank the Terres Australes et Antarctiques Françaises for their financial and logistical support throughout the study. The following people provided data: E. Ausilio, T. Chaurand, B. Derenne, L. Lemaire, J.-L. Mougín, P. Prince, V. Ridoux, J.-C. Stahl, C. R. Viot, H. Weimerskirch, and E. J. Woelher. Fieldwork in New Zealand was facilitated by A. J. Bartle and M. J. Imber. The diets were analyzed by V. Ridoux, L. Ruchon, and T. Chaurand. Recordings of prions from New Zealand were kindly provided by J. Kendrick and L. MacPherson. We are greatly indebted to A. J. Bartle and J. P. Croxall, who suggested many helpful improvements to earlier versions. Finally, we thank H. Weimerskirch and two anonymous referees for improving the manuscript, L. Ruchon for the figures, and C. P. Doncaster for the English version.

#### LITERATURE CITED

- AVISE, J. C., & R. M. ZINK. 1988. Molecular genetic divergence between avian sibling species: King and Clapper rails, Long-billed and Short-billed dowitchers, Boat-tailed and Great-tailed grackles, and Tufted and Black-crested titmice. *Auk* 105: 516-528.
- BERRUTI, A. 1981. The status of the Royal Penguin and Fairy Prion at Marion Island, with notes on feral cats predation on nestlings of large birds. *Cormorant* 9: 123-128.
- , & S. HUNTER. 1986. Some aspects of the breeding biology of Salvin's Prion *Pachyptila vittata salvini* at Marion Island. *Cormorant* 13: 98-106.
- BOURNE, W. R. P. 1987. The classification and nomenclature of the petrels. *Ibis* 129: 404.
- BRETAGNOLLE, V. In press a. Affinities of genus *Halobaena* (Procellariiformes) deduced from its behaviour. *Ibis*.
- . In press b. Calls of Wilson's Storm Petrel: functions, individual and sexual recognitions, and geographic variation. *Behaviour*.
- BROOKE, M. DE L. 1978. Sexual differences in the voice and individual recognition in the Manx Shearwater (*Puffinus puffinus*). *Anim. Behav.* 26: 622-629.
- . 1986. The vocal system of two nocturnal burrowing petrels, the white-chinned *Procellaria aequinoctialis* and the grey *P. cinerea*. *Ibis* 128: 502-512.
- BROTHERS, N. P. 1986. Breeding, distribution and status of burrow-nesting petrels at Macquarie Island. *Australian Wildl. Res.* 11: 113-131.
- CORBIN, K. W. 1983. Genetic structure and avian systematics. *Curr. Ornithol.* 1: 211-244.
- COX, J. B. 1980. Some remarks on the breeding distribution and taxonomy of the prions (Procellariidae: *Pachyptila*). *Rec. South Australian Mus.* 18: 91-121.
- CROXALL, J. P., S. MACINNES, & P. A. PRINCE. 1984. The status and conservation of seabirds at the Falkland Islands. Pp. 271-292 in *Status and conservation of the world seabirds* (J. P. Croxall, P. G. H. Evans, and R. W. Schreiber, Eds.). Cambridge, ICBP Technical Publ. 2.
- , P. A. PRINCE, I. HUNTER, S. J. MACINNES, & P. G. COPESTAKE. 1984. The seabirds of the antarctic peninsula, islands of the Scotia Sea, and antarctic continent between 80°W and 20°W: their status and conservation. Pp. 637-666 in *Status and conservation of the world seabirds* (J. P. Croxall, P. G. H. Evans, and R. Schreiber, Eds.). Cambridge, ICBP Technical Publ. 2.
- DERENNE, P. H., & J.-L. MOUGIN. 1976. Les Procellariiformes à nidification hypogée de l'île aux Cochons (archipel Crozet, 46°46'S, 50°14'E). *Comm. Natl. Français Rech. Antarctiques* 40: 149-176.
- DESPIN, B., J.-L. MOUGIN, & M. SEGONZAC. 1972. Oiseaux et mammifères de l'île de l'Est. *Comm. Natl. Français Rech. Antarctiques* 31: 1-106.
- DOBZHANSKY, T. 1937. *Genetics and the origin of species*. New York, Columbia Univ. Press.
- FALLA, R. A. 1940. The genus *Pachyptila* Illiger. *Emu* 40: 218-236.
- FLEMING, C. A. 1939. Birds of the Chatham Islands, 1. *Emu* 38: 380-412.
- . 1941. The phylogeny of the prions. *Emu* 41: 134-155.
- FULLAGAR, P. J. 1972. Identification of Prions—*Pachyptila* spp. *Australian Bird Bander* 10: 36-39.
- HARPER, P. C. 1972. The field identification and dis-

- tribution of the Thin-billed Prion (*Pachyptila belcheri*) and the Antarctic Prion (*P. desolata*). *Notornis* 19: 56-60.
- . 1976. Breeding biology of the Fairy Prion (*Pachyptila turtur*) at the Poor Knights Islands, New Zealand. *New Zealand J. Zool.* 3: 351-371.
- . 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.
- GUILLOTIN, M., & P. JOUVENTIN. 1980. Le Pétrel des Neiges à Pointe Géologie. *Gerfaut* 70: 51-72.
- JOUVENTIN, P. 1982. Visuals and vocal signals in penguins, their evolution and adaptive characters. *Advances in Ethology* 24. Berlin, Paul Parey.
- , J.-C. STAHL, H. WEIMERSKIRCH, & J.-L. MOUGIN. 1984. The seabirds of the French subantarctic islands and Adélie Land: their status and conservation. Pp. 609-626 in *Status and conservation of the world seabirds* (J. P. Croxall, P. G. H. Evans, and R. Schreiber, Eds.). Cambridge, United Kingdom, ICBP Technical Publ. 2.
- , & C. R. VIOT. 1985. Morphological and genetic variability in the Snow Petrel. *Ibis* 127: 430-441.
- , J.-L. MOUGIN, J.-C. STAHL, & H. WEIMERSKIRCH. 1985. Comparative biology of the burrowing petrels of the Crozet Islands. *Notornis* 32: 157-220.
- , V. RIDOUX, J.-C. STAHL, & H. WEIMERSKIRCH. 1988. La ségrégation écologique entre les pétrels des îles Crozet. *Terre et Vie* 43: 29-38.
- KINSKY, F. C., & P. C. HARPER. 1968. Shrinkage of bill-width in skins of some *Pachyptila* species. *Ibis* 110: 100-102.
- KNOX, A. G., & D. W. SNOW. 1987. The correct usage of the term "taxon." *Ibis* 129: 116.
- MCKITRICK, M. C., & R. M. ZINK. 1988. Species concepts in ornithology. *Condor* 90: 1-14.
- MATHEWS, G. M. 1912. *Birds of Australia*, vol. 2. London, Witherby.
- . 1938. *Pachyptila*, or the prions. *Emu* 37: 280-284.
- MAYR, E. 1970. *Populations, species and evolution*. Cambridge, Massachusetts, Belknap Press.
- . 1982. *The growth of biological thought*. Cambridge, Massachusetts, Belknap Press.
- MOUGIN, J.-L. 1985. Pétrels, pétrels-tempête et pétrels-plongeurs de l'île de Croy, îles Nuageuses, archipel des Kerguelen (48°38'15"S, 68°38'30"E). *L'Oiseau R.F.O.* 55: 313-349.
- MURPHY, R. C. 1936. *Oceanic birds of South America*, vol 1. New York, Am. Mus. Nat. Hist.
- NEI, M. 1975. *Molecular population genetics and evolution*. Amsterdam, North Holland Publ. Corp.
- PRINCE, P. A., & J. P. CROXALL. 1983. *Birds of South Georgia: new records and re-evaluation of status*. *Br. Antarctic Surv. Bull.* 59: 15-27.
- RANDI, E., F. SPINA, & B. MASSA. 1989. Genetic variability in *Cory's Shearwater* (*Calonectris diomedea*). *Auk* 106: 411-417.
- RICHDALE, L. E. 1944. The Titi Wainui or Fairy Prion *Pachyptila turtur* (Kuhl). *Trans. R. Soc. New Zealand.* 74: 32-48, 165-181.
- . 1965. Breeding behaviour of the Narrow-billed Prion and the Broad-billed Prion on Whero Island, New Zealand. *Trans. Zool. Soc. London* 31: 87-155.
- ROBERTSON, C. J. R., & B. D. BELL. 1984. Seabird status and conservation in the New Zealand region. Pp. 573-586 in *Status and conservation of the world seabirds* (J. P. Croxall, P. G. H. Evans, and R. Schreiber, Eds.). Cambridge, ICBP Technical Publ. 2.
- ROUNSEVELL, D. E., & N. P. BROTHERS. 1984. The status and conservation of seabirds at Macquarie Island. Pp. 586-592 in *Status and conservation of the world seabirds* (J. P. Croxall, P. G. H. Evans, and R. Schreiber, Eds.). Cambridge, ICBP Technical Publ. 2.
- ROUX, J.-P., J.-L. MOUGIN, & J. A. BARTLE. 1986. Le Prion de MacGillivray. *Données taxinomiques. L'Oiseau R.F.O.* 56: 379-383.
- , & J. MARTINEZ. 1987. Rare, vagrant and introduced birds on Amsterdam and Saint Paul islands, Southern Indian Ocean. *Cormorant* 14: 3-19.
- SERVENTY, D. L., V. SERVENTY, & J. WARHAM. 1971. *The handbook of Australian Seabirds*. Sydney, Reed.
- SIBLEY, C. G., & J. E. AHLQUIST. 1981. The phylogeny and relationships of the ratite birds as indicated by DNA-DNA hybridization. Pp. 301-355 in *Evolution today*, Proc. 2nd. Int. Congr. Syst. Evol. Biol. (G. G. E. Scudder and J. L. Reveal, Eds.). Pittsburgh, Hunt Inst. Botanical Documentation, Carnegie-Mellon Univ.
- , ———, & B. L. MONROE. 1988. A classification of the living birds of the world based on DNA-DNA hybridization studies. *Auk* 105: 409-423.
- STAHL, J.-C., P. JOUVENTIN, J.-L. MOUGIN, J.-P. ROUX, & H. WEIMERSKIRCH. 1985. The foraging zones of the seabirds in the Crozet Islands sector of the Southern Ocean. Pp. 478-486 in *Antarctic nutrient cycles and food webs* (W. R. Siegfried, P. R. Condy, and R. M. Laws, Eds.). Berlin, Springer-Verlag.
- STRANGE, I. J. 1980. The Thin-billed Prion, *Pachyptila belcheri*, at New Island, Falkland Islands. *Gerfaut* 70: 411-445.
- TICKELL, W. L. N. 1962. The Dove Prion *Pachyptila desolata* Gmelin. *Falkland Isl. Depend. Surv. Sci. Rep.* 33: 1-55.
- TOLLU, B. 1984. La Quille (Île Saint Paul, Océan Indien), sanctuaire de populations relictées. *L'Oiseau R.F.O.* 54: 79-85.
- WEIMERSKIRCH, H., R. ZOTIER, & P. JOUVENTIN. 1989. The avifauna of the Kerguelen Islands. *Emu* 89: 15-29.
- WILLIAMS, A. J. 1984. The status and conservation

on some islands in the African sector of the Southern Ocean. Pp. 627-636 in *Status and conservation of the world seabirds* (J. P. Croxall, P. G. H. Evans, and R. Schreiber, Eds.). Cambridge, ICBP Technical Publ. 2.

ZINK, R. M. 1988. Evolution of Brown Towhees: allozymes, morphometrics and species limits. *Condor* 90: 72-82.

## REVIEWERS FOR *THE AUK*, 1989

*The prepublication review process is essential to the maintenance of high scientific standards in a journal. The efforts of the individuals who contributed reviews, both singly and together, are remarkable. Each has been thanked personally, but deserves this public acknowledgment. The memorials for Volume 106 were solicited and managed by C. Stuart Houston. Individuals who contributed two or more manuscript reviews are signified with an asterisk.*

Ralph Ackerman, Alan D. Afton,\* David G. Ainley, Rauno V. Alatalo,\* Todd Arnold,\* G. Baeyens, Allan Baker, Robert J. Baker, Murray R. Bakst, Thomas G. Balgooyen, Gregory F. Ball, Martha Balph,\* G. Thomas Bancroft, Richard C. Banks,\* George F. Barrowclough, Thomas S. Baskett, Bruce Beehler, Colin Beer, Les Beletsky, P. Berthold, Louis B. Best, Verner P. Bingman,\* David M. Bird, Eric Bitterbaum, Gilbert W. Blankespoor, Cynthia K. Bluhm, Lawrence J. Blus, J. Sherman Boates, Carl E. Bock, Walter Bock, E. K. Bollinger, Patricia Blair Bollinger, Sarah W. Bottjer, Clait E. Braun, Eldon J. Braun, Randall Breitwisch, Margaret Brittingham, Charles R. Brown, Jerram L. Brown, Richard G. B. Brown, D. H. Brunton, D. M. Bryant, Theresa L. Bucher, F. G. Buckley, Deborah Buitron, Alan E. Burger, Ronald G. Butler, G. Vernon Byrd, Donald F. Caccamise,\* Angelo Capparella, Harry R. Carter, Yosef Cohen, Nicholas E. Collias, Charles T. Collins, Scott Collins, Michael W. Collopy, Mark Colwell,\* Richard N. Conner, Richard Coon, Susan E. Cosens, D. P. Costa, John C. Coulson, Malcolm Coulter,\* George W. Cox, Joel Cracraft, Thomas W. Custer, Randall Davis, Michael J. DeJong, David DeSante, Toni DeSanto, Andre Descrochers, Jared Diamond, Richard A. Dolbeer, H. Drummond, Alfred M. Dufty Jr., John Eadie, M. J. Eberhard, Scott Edwards,\* Tom Edwards, William R. Edwards, Stephen T. Emlen, Steven D. Emslie, Roger M. Evans, Susan Everts, Deborah M. Finch, Peter C. Frederick, Leonard Freed, Scott Freeman, Stephen D. Fretwell, Steve Funderburk, Philip K. Gaddis, Sarah B. Gaines, C. Lee Gass, Sidney A. Gauthreaux, Douglas C. Gayou, T. L. George, James A. Gessaman, Michael Gochfeld, David L. Goldstein, Bradley M. Gottfried, Gary R. Graves,\* Russell Greenberg, P. W. Greig-Smith, T. C. Grubb Jr.,\* Thaddeus Grudzien, Joseph A. Grzybowski, Carola A. Haas, Svein Haftorn, John M. Hagan, Susan Haig, Yrjö Haila, George Hall,\* Alan M. Hastings, Jeremy J. Hatch, Mickey E. Heitmeyer,\* Carl W. Helms, Gary R. Hepp, Gudrun Hilgerloh, David H. Hirth, Keith A. Hobson, Janet Hodder, Wayne Hoffman, A. J. Hogan-Warburg, William L. Hohman, Larry C. Holcomb, Geoffrey L. Holroyd, Dominique G. Homburger, Peter Houde, C. Stuart Houston, Marshall A. Howe, Robert W. Howe, Daryl Howes-Jones, John P. Hubbard, George L. Hunt Jr., Richard Hutto, I. R. Inglis, Danny J. Ingold, Douglas James, Frances Crews James, Donald A. Jenni, Paul A. Johnsgard, Ned K. Johnson, Richard F. Johnston, H. Lee Jones, R. L. Jones, David E. Joyner,\* William Karasov, A. A. Karlin, James R. Karr, Donald W. Kaufman, J. Allen Keast, Michael D. Kern, Ellen D. Ketterson, Mark Kirkpatrick, Richard L. Knight, Alan G. Knox, Walter D. Koenig, James A. Kushlan,\* Steve C. Latta, Marcy F. Lawton, Charles F. Leck, Robert E. Lemon,\* Sara Lenington, Jill Lightbody,\* James R. Lovvorn, Peter Lowther, Jeffrey Lucas, Arne Lundberg, Sheldon Lustick, Charles D. MacInnes, David A. Manuwal, J. Ellen Marsden, Joe T. Marshall, Carl D. Marti, Elden W. Martin, Steven Martindale, Carlos Martínez del Río, Dirkan Masman, J. Russell Mason,\* Barbara W. Massey, Sonke Mastrup, Brian A. Maurer, Stephen Maxson, Peter K. McGregor, Mary C. McKittrick, M. Robert McLandress, J. McLelland, Brooke Meanley, Albert H. Meier, Neil B. Metcalfe, Alex L. A. Middleton, Burt L. Monroe Jr., William A. Montevicchi, Robert D. Montgomery, Michael C. Moore, Ralph D. Morris,\* R. I. G. Morrison, Douglass H. Morse, Eugene S. Morton, James E. Mosimann, Robert Moss, Michael P. Moulton, Helmut C. Mueller, Ronald Mumme, Michael T. Murphy, Bertram G. Murray Jr., J. Peter Myers, Gerald Niemi, Sven G. Nilsson, Ian Nisbet, Daniel Niven, Erica Nol, Val Nolan Jr., Barry R. Noon, Christopher J. Norment, Raymond J. O'Connor, Robert D. Ohmart, Gordon H. Orians, David T. Parkin, Dorothy P. Pashley, John T. Paul Jr., Olof Pehrsson, Jaroslav Picman, Frank A. Pitelka, Allen R. Place, A. Poole, Dennis M. Power, D. K. Price, Harold H. Prince, James S. Quinn, Patricia Parker Rabenold, Robert Raikow, John H. Rappole, Dennis G. Raveling, Roland L. Redmond, James V. Rensman Jr., Jake Rice, Terrell D. Rich, W. John Richardson, Wayne Richter, Scott K. Robinson, Daniel D. Roby, R. F. Rockwell, Christopher M. Rogers,\* John G. Rogers Jr., Stephen P. Rogers, Frank C. Rohwer, Terry Root, Tim Roper, Roland R. Roth, Donald H. Rusch, Stephen M. Russell, Carl Safina,\* Paul Samollow, John Sauer, Rod Saylor, Thomas Schoener, D. M. Scott, Spencer G. Sealy, William A. Searcy, Fred Sheldon, Thomas W. Sherry, Gerald F. Shields, Gary Shugart, Paul Siegel, Douglas Siegel-Causey, Theodore R. Simons, Roy S. Slack, Tore Slagsvold, Chris Smith, Dwight Smith, Julia I. Smith, Noel F. R. Snyder, Keith M. Somers, Paul R. Sotherland, Jeffrey A. Spindelov, Peter B. Stacey,\* J. A. Stamps, Peter W. Stangel, Paul A. Stewart, Eric R. Stone, Robert W. Storer, Anne E. Storey, Phillip C. Stouffer, Bridget Stutchbury, Kimberly A. Sullivan,\* Per Sundberg, Bill Sydeman, Thomas C. Tacha, Betsy T. Thomas, Bruce Thompson, Charles F. Thompson,\* Rodger D. Titman, Kimberly Titus, Diana F. Tomback, Michael W. Tome, Michael H. Tove, Elliot J. Tramer, Angela K. Turner, Staffan Ulfstrand, Stephen B. Vander Wall,\* Gerald F. van Tets, Michael Wallace, Kenneth Warheit, Doris J. Watt, D. R. Webb,\* Thomas Webber, Marcus D. Webster, Nathaniel T. Wheelwright, G. Causey Whittow, Kathy Winnett-Murray, Rick Wishart, Glen E. Woolfenden, Andrea Worthington, Thomas Wray II, Richard L. Wyman, R. C. Ydenberg, Yoram Yom-Tov, Reto Zach, Patricia G. Zenone, John L. Zimmerman, Robert M. Zink.