

MORPHOLOGICAL DIFFERENCES RELATIVE TO ECOLOGICAL SEGREGATION IN PETRELS (FAMILY: PROCELLARIIDAE) OF THE SOUTHERN OCEAN AND TROPICAL PACIFIC

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ABSTRACT.—We compared eight morphological characters (wing span, wing area, aspect ratio, tail length, bill length, bill depth, tarsus length, and mass of subcutaneous/mesenteric fat) among petrels (family Procellariidae) of tropical versus southern polar avifaunas. Relative to body mass, tropical species have larger wings, bills, and tails, and lighter fat reserves than do polar species. We attributed these differences primarily to adaptations for feeding in markedly different pelagic environments. Larger wings, bills, and tails of tropical species enable them to make use of relatively light winds when foraging over wide ocean expanses to exploit sparse and highly mobile and/or volant prey. In contrast, the smaller wings, bills, and tails of polar species enable them to cope with strong winds to exploit highly abundant, less-mobile prey. Greater fat reserves among polar species probably are an adaptation for surviving extended periods when rough weather (rarely experienced by tropical species) precludes feeding, or for thermoregulation. The most consistent and marked differences between avifaunas are in wing structure and fat load—characters that are directly related to adaptations to physical factors such as wind and climate. Species-specific differences within avifaunas are mostly related to specializations for different foraging habits (i.e. feeding behavior, prey composition, and prey size). Morphological differences and within-species character variances indicated that the tropical ocean is used by a more generalist, migratory group of petrels, whereas the Southern Ocean is used by a more specialized, resident group of petrels. *Received 20 October 1997, accepted 17 April 1998.*

NO SPECIES comprising the tropical and polar avifaunas of the South Pacific occupy both habitats (Ainley and Boekelheide 1983, Ribic and Ainley 1989), suggesting specialization among members of each avifauna for existence in their respective regimes. Such specialization should arise from differences in selective factors, including differences in breeding and feeding habitat, predators, and weather/climate (Mayr 1963, Bock 1974, Ainley 1977, Krebs and Houston 1989). Whatever these adaptations are, and few have been studied in detail (Warham 1990, 1996), they should be reflected by differences in morphology as noted for other avian groups (James 1982). Thus, a morphological comparison of species within the two avifaunas should help to identify the degree of specialization and factors responsible for their distinctness.

Within the family Procellariidae, we compared morphology of species of petrels that predominate in the eastern tropical Pacific (ETP; nine species) with those that predominate in polar latitudes of the Southern Ocean (seven species). The 16 species share three fun-

damental life-history traits: (1) all are strictly pelagic throughout the year, (2) they have similar breeding habits, and (3) the overlap in prey species is extensive within each avifauna (Imber 1985, Ainley et al. 1991, 1992; Rau et al. 1992, Ainley and Spear unpubl. data). Therefore, we assume that differences in morphology should reflect mostly, if not entirely, adaptations for exploiting marine environments that differ both physically and biologically, and/or for existence in different climates.

To identify environmental features that are likely to structure morphological adaptations of the two avifaunas, we compared the length of the wings, tail, and legs; bill shape (length and depth); wing area (relative to body mass); and aspect ratio (wing shape) between and among species of the two avifaunas. We also compared differences in the amount of fat reserves as an indicator of climatic stress (see Lima 1986), and as a factor affecting body mass.

METHODS

We examined most of the small to medium-sized species of petrels (mass <0.8 kg) that inhabit the ETP

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TABLE 1. Species composition (proportion of the total number recorded) of procellariids (not including shearwaters and migrants) recorded during surveys in the eastern tropical Pacific and Southern Ocean. Asterisks denote species included in the current analysis. Observations of tropical species occurred between 20°N and 20°S and 110° to 170°W; those of polar species occurred south of 55°S. Total count, after adjustment for bird movement relative to that of ship (Spear et al. 1992), was 12,584 individuals of tropical species and 28,260 individuals of polar species.

Tropical species	%	Polar species	%
Juan Fernandez Petrel (<i>Pterodroma externa</i>)*	56.0	Snow Petrel (<i>Pagodroma nivea</i>)*	24.6
Black-winged Petrel (<i>P. nigripennis</i>)*	16.7	Antarctic Petrel (<i>Thalassoica antarctica</i>)*	23.0
White-winged Petrel (<i>P. leucoptera</i>)*	12.2	Southern Fulmar (<i>Fulmarus glacialisoides</i>)*	18.1
Tahiti Petrel (<i>P. rostrata</i>)*	5.7	Cape Petrel (<i>Daption capense</i>)*	12.6
Bulwer's Petrel (<i>Bulweria bulwerii</i>)*	4.3	Prions (<i>Pachyptila</i> spp.)	11.6
White-necked Petrel (<i>P. cervicalis</i>)*	1.7	Blue Petrel (<i>Halobaena caerulea</i>)*	7.7
Kermadec Petrel (<i>P. neglecta</i>)*	1.5	Kerguelen Petrel (<i>Pterodroma brevirostris</i>)*	0.8
Phoenix Petrel (<i>P. alba</i>)*	1.0	Mottled Petrel (<i>P. inexpectata</i>)*	0.8
Herald/Henderson Petrel (<i>P. heraldica/atrata</i>)*	0.7	Giant Petrels (<i>Macronectes</i> spp.)	0.7
Collared Petrel (<i>P. brevipes</i>)	0.1	White-Chinned Petrel (<i>Procellaria aequinoctialis</i>)	0.1
Pycroft's Petrel (<i>P. pycrofti</i>)	0.1		

(hereafter "tropical" species; not including species that migrate through the tropical ocean to northern wintering areas) and polar waters (south of 55°S) of the Southern Ocean (hereafter "polar" species). We confined our analyses to a given size range of species because: (1) species of highly pelagic, seasonally resident procellariids larger than 0.55 kg do not inhabit the tropics, and (2) we wished to confine our comparison to species of a similar trophic level to better standardize the study group ecologically. Thus, we excluded the larger polar procellariids (*Macronectes* and *Procellaria*). The species we examined composed 99.8%, and 87.6%, respectively, of all procellariid petrels recorded during cruises in the ETP (1983 to 1995), and in the Scotia-Weddell, Ross, and Amundsen-Bellinghousen seas of the Southern Ocean during 1978 to 1996 (Table 1). The remaining 0.2% of the at-sea sightings of tropical species that we did not examine were the Pycroft's Petrel (*Pterodroma pycrofti*) and Collared Petrel (*P. brevipes*), which were omitted owing to small samples of specimens. The remaining 12.4% of the at-sea sightings of polar procellariids not examined were either larger than 0.8 kg (see above) or were prions (genus *Pachyptila*) that were omitted because of small sample sizes.

The phylogeny of these petrels is controversial (see Imber 1985, Warham 1990). Following the AOU (1983), Warham (1990), and Brooke and Rowe (1996; for Herald [*P. heraldica*]/Henderson [*P. atrata*] petrels), tropical species included eight of the genus *Pterodroma* (= gadfly petrels) and the Bulwer's Petrel (*Bulweria bulwerii*; Table 1). Although the Tahiti Petrel (*P. rostrata*) was split from *Pterodroma* and classified as *Pseudobulweria rostrata* (Mathews 1942, Imber 1985) based on gut morphology, feather lice, and skull characteristics, we followed Warham (1990) and listed it among the gadfly petrels. We grouped the Herald and Henderson petrels (hereafter "Herald Petrel") because of their similarity (Brooke 1995,

Brooke and Rowe 1996), and because our samples of each were too small for separate analyses. The seven polar species represent seven genera, five of which are monospecific (Table 1). Four are considered of close phylogenetic origin (= fulmarine petrels; Warham 1990), including the Southern Fulmar (*Fulmarus glacialisoides*), Antarctic Petrel (*Thalassoica antarctica*), Cape Petrel (*Daption capense*), and Snow Petrel (*Pagodroma nivea*). The Mottled Petrel (*Pterodroma inexpectata*) and Kerguelen Petrel (*P. brevirostris*) are considered to be gadfly petrels (Warham 1990), although Imber (1985), placed the Kerguelen Petrel in the monospecific genus, *Lugensa*. The lineage of the Blue Petrel (*Halobaena caerulea*) is thought to lie somewhere between *Pterodroma* and *Pachyptila* (Warham 1990, 1996).

We collected 203 specimens in polar waters of the Southern Ocean during the nonbreeding season (July to August), and 656 specimens in the ETP during April to July and October to December. Only Tahiti Petrels, Phoenix Petrels (*P. alba*), and Bulwer's Petrels breed in the ETP; thus, most tropical species were in their nonbreeding season as well. We gathered data on petrel feeding methods during cruises in the ETP and Southern Ocean. Data reported include all observations, including those of Ainley et al. (1984).

Spear determined the sex of each specimen by inspecting the gonads, and measured five morphological characters (mm): tail length (length of the central rectrices from insertion to distal tip), tarsus length, bill length (distance from proximal edge to most distal surface of the rhamphotheca), and bill depth (width of the closed bill from the top of the upper mandible just in front of the nares to the surface directly below on the bottom of the lower mandible). We recorded body mass (g), excluding stomach contents, and calculated the surface area of the wings (cm²) and wing aspect ratios following Pennycuik (1989:10-14), except that the area of the body be-

tween the wings was not included in measurements of wing area (these are given in Spear and Ainley 1997a). To measure wing span (length from tip to tip of fully extended wings of birds placed on their backs) and wing area (see "right method" in Pennycuik 1989: figure 2.3), we relaxed the pectoral muscles of birds with rigor-mortis before extending the wings. This was done by slowly extending the wings forward and upward with a thumb placed on the ventral side of the humerus just above the base of the wing (where the wings attach to the body). Wing measurements of birds molting their 10th primaries were not used. To standardizing wing areas as the maximum area obtained during the annual cycle, we traced wing profiles of birds molting inner primaries and secondaries as though the feathers were not missing; i.e. profile tracings were drawn (interpolated) across gaps where feathers were missing or growing. This practice did not affect the accuracy of measurements because gaps were not large and were easily interpolated.

To compare fat loads, Spear scored subcutaneous fat deposits of each specimen after partially skinning them. Fat load was scored as follows: 0 = no fat or traces only; 1 = light deposit near hind limbs and abdomen but absent or mostly absent over the pectoral muscles; 2 = light deposit continuous or mostly continuous over the pectoral muscles; 3 = moderate deposit throughout; and 4 = heavy deposit throughout.

To evaluate the scored indices of fat load quantitatively, we removed subcutaneous and mesenteric fat (SMF) deposits from a subset of 141 specimens for which fat loads had been scored. All species except the Herald Petrel were represented in the samples for quantitative examination of SMF, the mass of which was estimated as follows. Solid fat and oil of skinned specimens were thoroughly excised from the entire skin, surface of the body, and abdominal cavity. Any remaining oil was blotted from the skin with a pre-weighed paper towel, its mass determined and added to that of the solid fat and oil already removed. We estimate that we were unable to remove up to 5% of SMF from specimens with fat indices of 1, but that the proportion of fat not removed decreased to <1% in very fat birds. There was a low incidence of overlap (error) in values of percent SMF as a function of fat score (6 in 141 scores, or 4.3%; Fig. 1), and overlap occurred only in the low end of the index where differences in SMF load were small. Therefore, our method of scoring SMF was reliable.

Each linear character was "scaled" (i.e. standardized; see Ingólfsson 1967, Pennycuik 1992) by dividing the measured value by the cube root of body mass. For an index of wing surface area, the square root of the wing area was divided by the cube root of body mass. Aspect ratio is a dimensionless index of wing shape (Pennycuik 1989). Scaled character values of the polar species were affected more by fat

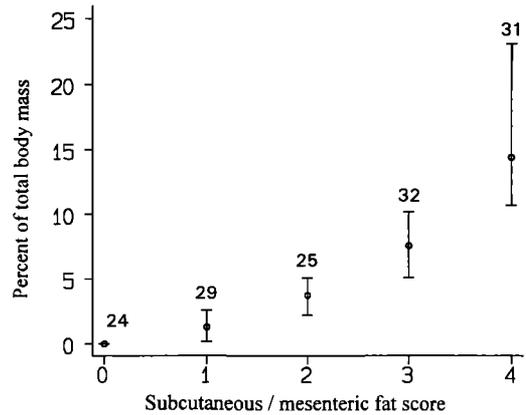


FIG. 1. Mean subcutaneous and mesenteric fat (SMF) load (expressed as percent of body mass) as a function of fat load index scored by visual examination of specimens. Values are means and ranges. Numbers above vertical bars are sample sizes.

load than were values of tropical species, because polar species were fatter. To compare the effect of fat load on morphological characters, we calculated scaled characters on both a "fresh-mass" and "lean-mass" basis, where lean mass = fresh mass - SMF. We estimated SMF mass for specimens for which we had only scored SMF by multiplying body mass by the mean percent SMF as determined for each fat score among specimens examined quantitatively for SMF (Fig. 1).

We compared pectoral mass (= mass of both pectoralis major and pectoralis minor) in a subset of 116 specimens representing six tropical species. All specimens were healthy when collected (i.e. not emaciated). Pectorals were removed from fresh specimens and weighed, after which we calculated an index by dividing pectoral mass by lean body mass.

Analyses.—Because species are part of a hierarchical branching phylogeny, they may share traits solely because of common ancestry. Therefore, especially when species are closely related, assessing differences in traits among species as though the species were independent may overestimate the degrees of freedom and, thus, statistical significance (Felsenstein 1985, Martins and Garland 1991). Although the confounding effects of phylogeny can be removed by converting the data into phylogenetically independent contrasts (Felsenstein 1985), we did not attempt this because these methods are controversial (Pagel and Harvey 1992, Purvis et al. 1994), and because petrel phylogeny is poorly known (see above). However, we address this problem through special attention to the relationships between tropical and polar *Pterodroma*, and using other factors (see Discussion).

Statistical analyses were performed using STATA (STATA 1995). Summary statistics for body mass, fat

load, aspect ratio, and non-scaled (raw) morphological characters are given in the Appendix. We used regression analyses to compare all morphological characters (the dependent variables) between the tropical and polar species. We used the scaled character values for comparisons of bill length, bill depth, tarsus length, tail length, wing length, and wing area (see above). Because distributions of the scaled characters (by species) satisfied assumptions of normality, no statistical transformations were needed. To control for unequal sample sizes among species, we used species as the sample unit. Thus, the sample n for each regression was 16 species. To control for species' character variances, each analysis included the weighting of species' character means by the reciprocal of the standard error. For these analyses, tropical species were assigned a value of 1 and polar species a value of 2. Thus, a positive regression coefficient indicated that the character being compared was greater among polar versus tropical species, and vice versa for negative coefficients. Test for character differences among the 16 species were performed using Sidak multiple comparisons tests, an improved version of the Bonferroni test (SAS 1985).

We used principal components analysis (PCA), performed on values for six continuous characters (bill length, bill depth, tarsus length, wing span, wing area, and aspect ratio) at the individual level to determine if species were morphologically distinct. Because of missing data, tail length was excluded from the analyses. For each PCA, the means \pm 1 SD for the first and second PC axes were plotted, by species, to examine overlap in morphological structure. Only the first two principal components are used because they explained >60% of the variance. Our objective was to examine the possibility that species within and between habitats were responding to similar (or different) environmental factors. We would expect that each important selective factor would be expressed uniquely in the morphological adaptations of a given species, and that ecological specialists would exhibit less character variance than generalist species.

With exception of features including body mass, SMF fat, and aspect ratio, reference to size of morphological characters hereafter refers to the scaled values (i.e. the proportional relationship between the character and body mass), not to absolute values.

To evaluate the possibility that between-species differences in scaled character variances could reflect differences in the degree of sexual dimorphism (see van Franeker and ter Braak 1993), we computed an index of sexual dimorphism (DI) for each of six morphological characters for eight tropical species and five polar species (Mottled, Kerguelen, and Herald petrels were not included owing to small sample sizes). DIs were the mean scaled character for lean body mass of the females divided by that of the males \times 100. Pearson correlations were used to test

for a relationship among species of each avifauna between the mean DIs (averaged across the six characters for each species) and the character variances averaged across the PC1 and PC2 scores for each species. A significant correlation between the DIs and character variances would indicate that morphological variation among species was affected by sexual differences.

Five methods of feeding (defined in Ainley 1977) were recognized during observations at sea. We used Chi-square tests to compare frequency of use of feeding methods within and between avifaunas. For the between-avifaunas comparison, we summed the number of observations for each feeding method across the species in each avifauna. This weighted the analysis by each species' feeding frequency; i.e. species observed to have fed more often (generally the more abundant ones) were given more importance in the between-avifauna comparison.

RESULTS

Comparison of morphological characters between avifaunas.—Fat scores of polar species were significantly higher than those of tropical species (Table 2), with no overlap among species' fat-score variances between the two avifaunas (Fig. 2). Neither fresh mass nor lean mass differed significantly between avifaunas (Table 2).

Bill length, bill depth, tail length, wing span, and wing area were significantly larger in tropical species compared with polar species (Table 2, Figs. 3 and 4), whereas tarsus length and aspect ratio did not differ significantly between members of the two avifaunas. P -values for these relationships differed little between analyses based on fresh or lean mass (Table 2). Thus, a true structural difference occurred between the two avifaunas with respect to these characters. Morphological features differing the most between avifaunas were wing span and wing area. There was no overlap between the two groups for either character, although wing area of the Snow Petrel approached that of tropical species having smaller wing areas (Fig. 4).

Comparisons of morphological characters of gadfly petrels between avifaunas.—Except for bill length, tarsus length, and aspect ratio, morphological features of the two polar *Pterodroma* differed significantly from those of the eight tropical *Pterodroma* (Table 3, Figs. 2 to 4). Thus, polar *Pterodroma* had bills of smaller depth, shorter tails, shorter wings, smaller wing areas, and more fat compared with tropical *Pterodroma*.

TABLE 2. Univariate regression analyses comparing morphometric characters of nine tropical species of procellariids with those of seven southern polar species (i.e. $n = 16$ for each analysis). Scaled values for each linear character were calculated as the average across all individuals (see Appendix for sample sizes). "Fresh" denotes that mass of subcutaneous and mesenteric fat was included with body mass in scaling of character values; "lean" denotes that mass of fat was not included in scaling. Analyses were weighted, by species, by the reciprocal of the SE of character values. A positive regression coefficient indicates that the character was larger in polar species than tropical species, and vice versa for negative values.

Character	Coefficient	SE	F-value	P-value	R ²
Body mass					
Fresh	143	82.5	3.02	0.10	0.178
Lean	111	79.1	1.98	0.18	0.124
Fat score	2.2	0.33	42.41	<0.0001	0.752
Bill length					
Fresh	-0.86	0.33	14.67	0.002	0.512
Lean	-0.75	0.22	10.95	0.005	0.439
Bill depth					
Fresh	-0.17	0.05	10.82	0.005	0.436
Lean	-0.16	0.04	14.66	0.002	0.512
Tarsus length					
Fresh	-0.34	0.22	2.34	0.15	0.143
Lean	-0.22	0.23	0.87	0.40	0.059
Tail length					
Fresh	-2.70	1.12	5.83	0.03	0.294
Lean	-2.20	0.89	6.42	0.02	0.314
Wing span					
Fresh	-22.5	1.02	484.6	<0.0001	0.972
Lean	-18.3	1.33	189.0	<0.0001	0.931
Wing area					
Fresh	-0.54	0.07	63.47	<0.0001	0.819
Lean	-0.41	0.07	38.95	<0.0001	0.736
Aspect ratio	-0.18	0.38	0.24	0.60	0.018

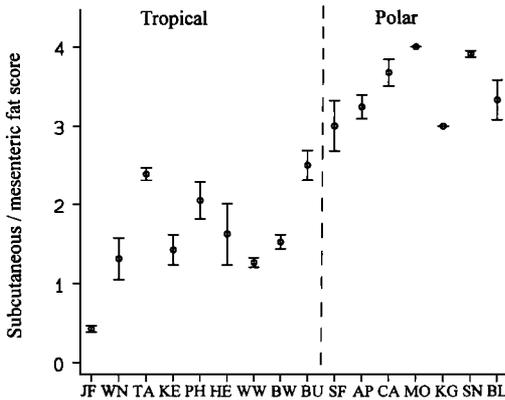


FIG. 2. Mean SMF score \pm SE of tropical and polar petrels. Species are: JF, Juan Fernandez Petrel; WN, White-necked Petrel; TA, Tahiti Petrel; KE, Kermadec Petrel; PH, Phoenix Petrel; HE, Herald Petrel; WW, White-winged Petrel; BW, Black-winged Petrel; BU, Bulwer's Petrel; SF, Southern Fulmar; AP, Antarctic Petrel; CA, Cape Petrel; MO, Mottled Petrel; KG, Kerguelen Petrel; SN, Snow Petrel; and BL, Blue Petrel. See Appendix for sample sizes.

However, each of the features of polar *Pterodroma* were similar to those of the other polar species (see Figs. 2 to 4).

Species differences within avifaunas.—The most distinct differences among the tropical petrels were the extremely long tarsus, very deep (i.e. robust) bill, high aspect ratio, and very small pectoral muscles of the Tahiti Petrel (which also had a high fat score, long bill, small wing area, and short tail; Figs. 2 to 6); the very long tail and large wing area of the Bulwer's Petrel (which also had a high fat score, long wings, and long tarsi); the very low fat load and long bill of the Juan Fernandez Petrel (*Pterodroma externa*; which also had a deep bill); the large wing area and long tail of the Black-winged Petrel (*P. nigripennis*), and very short tail of the Kermadec Petrel (*P. neglecta*).

The most distinct differences among the species of polar petrels were the very large wing area, long tail, and short bill of the Snow Petrel (which also had a low aspect ratio; Figs. 3 to 5); the long, deep bill, and short wings of the Southern Fulmar; and the extremely long tar-

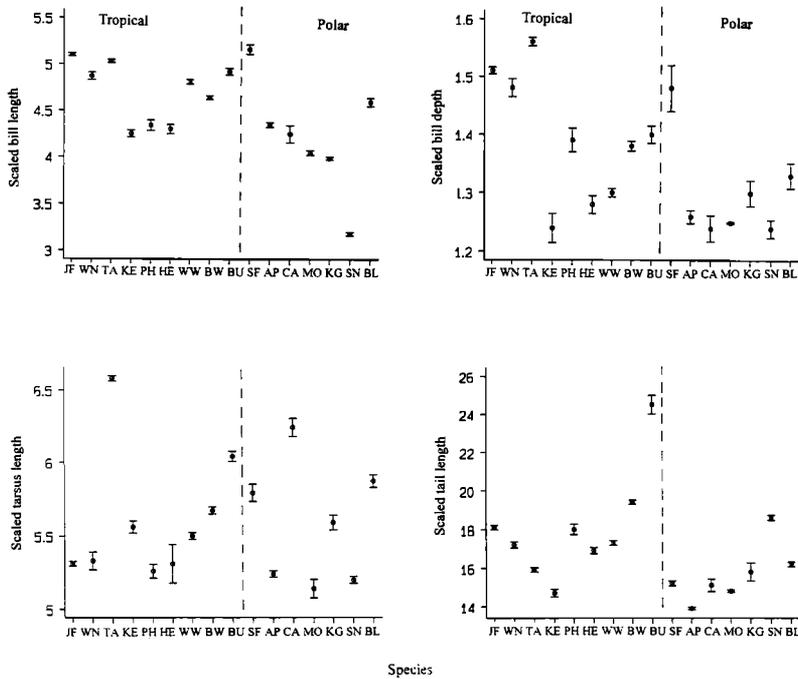


FIG. 3. Mean scaled values \pm SE of morphological characters including bill length, bill depth, tarsus and tail length of tropical and polar petrels. Species codes are given in Figure 2. See Appendix for sample sizes for each character.

sus of the Cape Petrel. Kerguelen Petrels and Antarctic Petrels also had very high aspect ratios.

Principal components analyses of morphological characters between avifaunas.—Because the effects of SMF on character relationships were insignificant, we performed PCA only on lean character values. There was no overlap between the two avifaunas when considering both axes simultaneously, but when considering each axis separately, there was moderate overlap (Fig. 7). For the PC1 axis, where the major variables (i.e. those having the most variability) were bill depth, bill length, and wing span (Table 4), most of the overlap between avifaunas was due to similarities between two of the nine tropical species (Kermadec Petrel and White-winged Petrel [*Pterodroma leucoptera*]) and five of the seven polar species (i.e. all except Snow Petrel and Mottled Petrel; Fig. 7). On the PC2 axis, where wing area and aspect ratio were the major variables (Table 4), there was overlap between the Tahiti Petrel and several polar species, and between the Snow Petrel and several tropical species (Fig. 7). The polar *Pterodroma*

were clustered among the other polar petrels, and, with slight exception of the Tahiti Petrel, were markedly distinct from the tropical *Pterodroma*.

Principal components analyses of morphological characters within avifaunas.—The Tahiti and Bulwer's petrels were distinct from one another and from the other tropical *Pterodroma*, which overlapped extensively (Fig. 8A). The distinctness of the Tahiti Petrel occurred on the PC1 axis, where bill depth, aspect ratio, and tarsus length were the most variable characters (Table 5). The Juan Fernandez and White-necked (*P. cervicalis*) petrels were mostly distinct from other *Pterodroma* on the first axis, but overlapped with the Phoenix Petrel (Fig. 8A). The Kermadec Petrel overlapped only with the White-winged Petrel. With exception of the Bulwer's Petrel, extensive overlap occurred among all tropical species on the PC2 axis, where wing area and wing span were the most variable characters (Table 5, Fig. 8A).

Among polar species, the Southern Fulmar, Mottled Petrel and, especially, the Snow Petrel, differed from one another and from the other

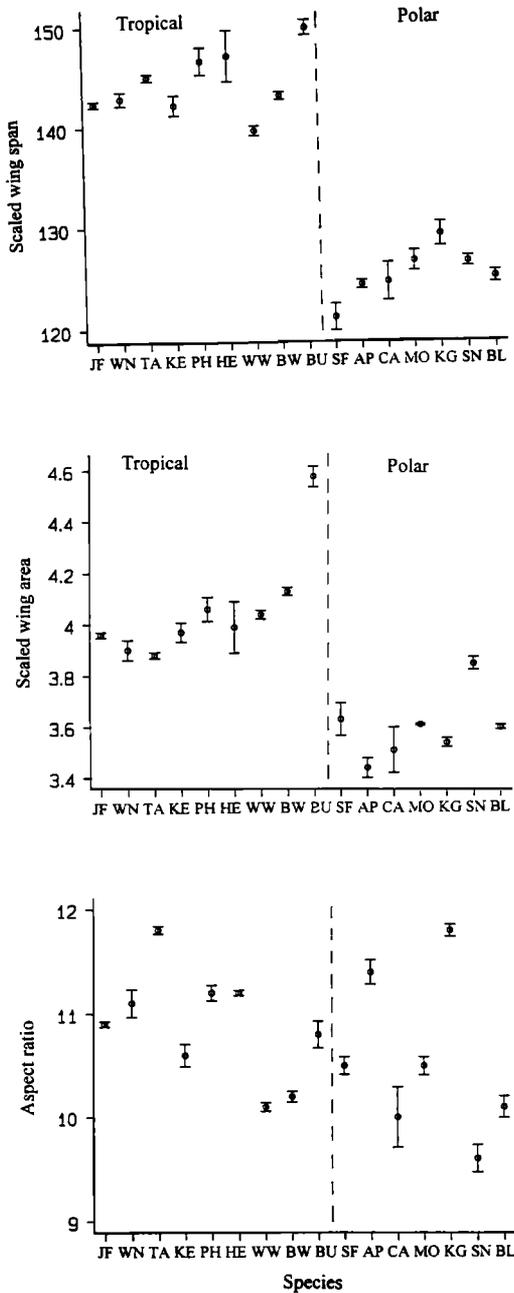


FIG. 4. Mean scaled values \pm SE of morphological characters including wing span, wing area, and aspect ratio of tropical and polar petrels. Species codes are given in Figure 2. See Appendix for sample sizes for each character.

species (Fig. 8B). Morphological characteristics of Antarctic Petrels and Kerguelen Petrels overlapped, as did those of Antarctic Petrels and Cape Petrels, and Blue Petrels and Cape Petrels. Separation of the Snow Petrel from the other polar species occurred on the PC1 axis, where bill length and wing area had the highest variability (Table 5). The Southern Fulmar and Mottled Petrel also differed on the first axis from other petrels except the Cape Petrel (Fig. 8B). More overlap occurred among polar species on the PC2 axis, where the most divergent characters were aspect ratio and bill depth (Table 5, Fig. 8B).

Compared with tropical species, variances of PC1 and PC2 scores (averaged together for each species) were significantly smaller among the polar species ($t = 2.28$, $df = 14$, $P = 0.039$; Fig. 7). Bulwer's Petrels and Phoenix Petrels had the highest variances in PC scores among the tropical species, whereas Herald Petrels and Black-winged petrels had the lowest variances. The Cape Petrel showed, by far, the highest variance among polar species, and the Mottled Petrel and Kerguelen Petrel had very low variances, followed closely by the Blue Petrel.

Sexual differences in body size and relation with scaled character variances.—Dimorphism indices within the tropical and polar avifaunas were very small (Table 6). Sexual differences between the scaled character values of the two avifaunas averaged 1.6% and 2.2%, respectively, a difference that was not significant ($t = 1.77$, $df = 11$, $P = 0.1$). Correlations between DIs and scaled-character variances for PC scores were also nonsignificant (tropical species, $r = 0.279$, $n = 8$, $P = 0.5$; polar species, $r = 0.546$, $n = 5$, $P = 0.3$; Table 6). Thus, the degree of morphological variation among species did not seem to be affected by sexual differences.

Feeding methods and feeding incidence.—Tropical and polar avifaunas differed significantly in frequency of use of five feeding methods ($\chi^2 = 971.6$, $df = 4$, $P < 0.0001$; Table 7). Tropical species frequently used aerial pursuit of volant prey but seldom "surface plunged," whereas the polar group used surface seizing, and especially surface plunging, but not aerial pursuit. Pursuit diving and piracy were used infrequently by members of both avifaunas. Feeding methods used most often by tropical species were, in order of decreasing importance,

TABLE 3. Univariate regression analyses comparing morphometric characters of eight tropical *Pterodroma* with those of two polar *Pterodroma* (i.e. $n = 10$ for each analysis). Scaled characters were calculated from lean body mass as the average across all individuals (see Appendix for sample sizes). Analyses were weighted, by species, by the reciprocal of the SE of character values. A positive regression coefficient indicates that the character was larger in polar *Pterodroma* than in tropical *Pterodroma*, and vice versa for negative values.

Character	Coefficient	SE	F-value	P-value	R ²
Fat score	2.70	0.26	107.36	<0.0001	0.931
Bill length	-0.53	0.28	3.65	0.092	0.314
Bill depth	-0.16	0.06	8.76	0.018	0.523
Tarsus length	-0.09	0.49	0.03	0.900	0.004
Tail length	-2.10	0.89	5.35	0.049	0.401
Wing span	-17.40	1.74	100.05	<0.0001	0.926
Wing area	-0.38	0.04	81.34	<0.0001	0.911
Aspect ratio	-0.62	0.59	1.09	0.300	0.120

aerial pursuit, surface seizing (including scavenging), and contact dipping/surface plunging. Polar species used surface seizing and contact dipping/surface plunging most frequently (Table 7).

Significant differences occurred between species of each avifauna in frequency of use of different feeding methods (tropical, $\chi^2 = 506.4$, $df = 24$, $P < 0.0001$; polar, $\chi^2 = 1,358$, $df = 18$, $P < 0.0001$; Table 7). Among the tropical spe-

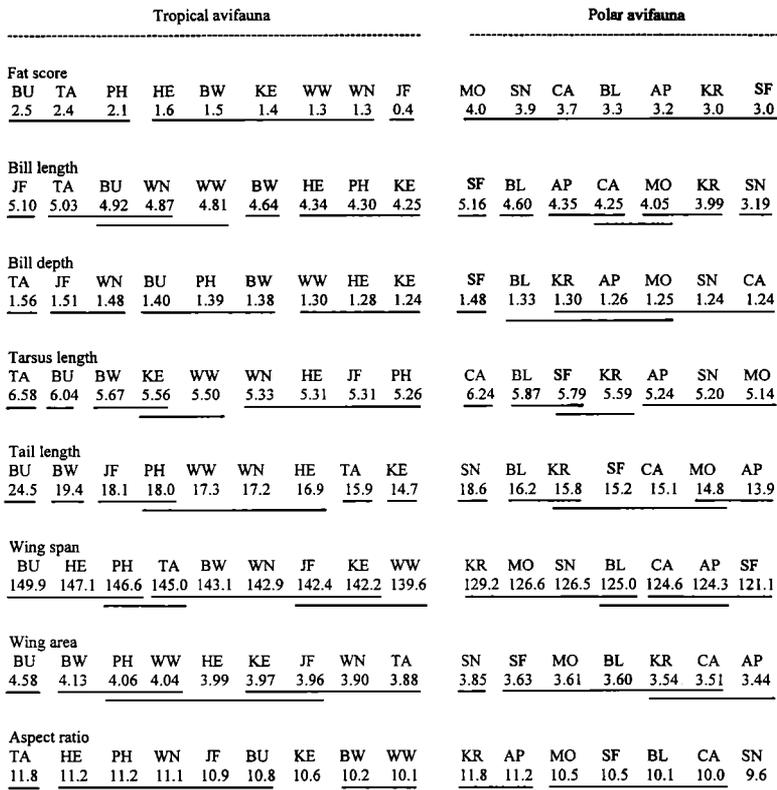


FIG. 5. Results of Sidak multiple comparisons tests for eight morphological characters compared among tropical species, and among polar species. Species codes are given in Figure 2. Values given below species codes are the mean scaled values. Lines not connected between adjacent species denote significant differences. See Appendix for sample sizes for each character.

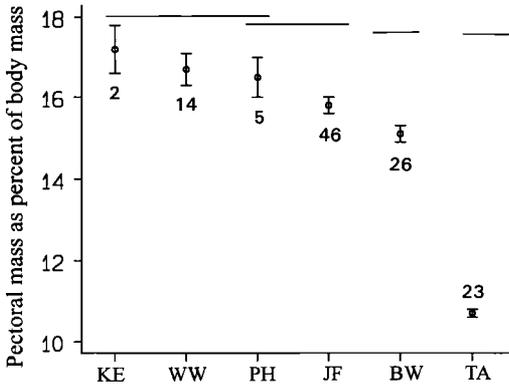


FIG. 6. Pectoral muscle mass (mean \pm SE) shown as the percent of the total lean body mass. Species codes are given in Figure 2. Lines not connected between adjacent species denote significant differences (Sidak multiple comparisons test; $P < 0.05$). Numbers are sample sizes.

cies, four (Tahiti, White-winged, Black-winged, and Bulwer's petrels) predominantly used surface seizing, and three (Juan Fernandez, White-necked, and Herald petrels) predominantly used aerial pursuit. Phoenix Petrels used surface plunging most frequently, and Kermadec Petrel used surface seizing and piracy in equal proportions.

Among the polar species, three (Antarctic, Snow, and Blue petrels) fed mostly by surface

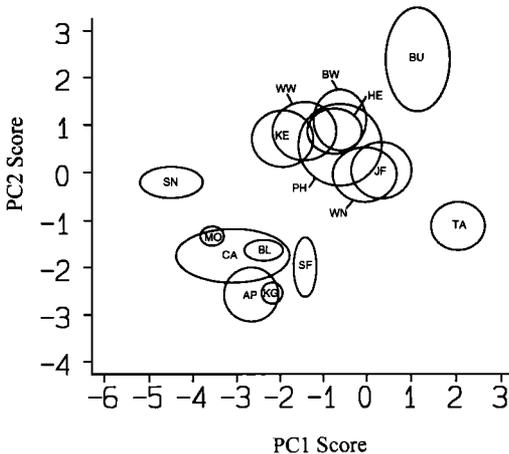


FIG. 7. PC1 and PC2 scores of 16 species of petrels, calculated from analyses that included values for six characters scaled by lean mass (see Table 4). Species codes are given in Figure 2. Circles around species codes are the standard deviations for the PC1 and PC2 scores.

TABLE 4. Eigenvector loadings from principal component analysis of six morphological characters of tropical and polar procellariids scaled by lean mass. Both avifaunas were included in the same analysis. PC1 explained 46% of the variance and PC2 an additional 29%. Sample sizes are given in the Appendix.

Character	PC1	PC2
Bill length	0.46	0.05
Bill depth	0.49	-0.21
Tarsus length	0.39	-0.16
Wing span	0.46	0.42
Wing area	0.17	0.73
Aspect ratio	0.40	-0.47

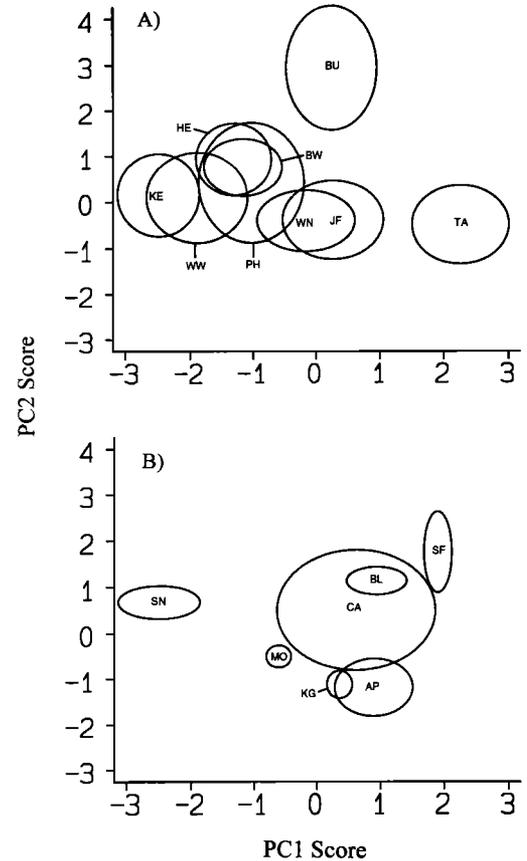


FIG. 8. PC1 and PC2 scores of (A) tropical petrels and (B) polar petrels, calculated from analyses that included values for six characters scaled by lean mass (see Table 4). Species codes are given in Figure 2. Circles around species codes are the standard deviations for the PC1 and PC2 scores.

TABLE 5. Eigenvector loadings from principal component analysis of six morphological characters of tropical and polar procellariids scaled by lean mass. Tropical and polar avifaunas were analyzed separately. For tropical species, PC1 explained 44% of the variance and PC2 an additional 28%; for polar species, PC1 explained 40% of the variance and PC2 an additional 25%. Sample sizes are given in the Appendix.

Character	Tropical species		Polar species	
	PC1	PC2	PC1	PC2
Bill length	0.42	0.04	0.58	0.14
Bill depth	0.52	-0.15	0.25	0.53
Tarsus length	0.44	0.13	0.34	0.34
Wing span	0.34	0.58	-0.36	-0.21
Wing area	-0.08	0.74	-0.50	0.44
Aspect ratio	0.49	-0.26	0.32	-0.59

plunging, and two (Southern Fulmar and Cape Petrel) fed mostly by surface seizing (Table 7). We observed few instances of feeding by Kerguelen Petrels and Mottled Petrels. Both species fed by pursuit diving and by surface plunging (Kerguelen Petrel) and surface seizing (Mottled Petrel). Antarctic Petrels also occasionally used pursuit diving.

Feeding incidence (the number of feeding birds per total number observed) was signifi-

cantly higher among polar species than among tropical species ($\chi^2 = 74.0$, $df = 1$, $P < 0.0001$; Table 7); however, feeding incidence differed significantly among species composing each avifauna (tropical, $\chi^2 = 62.9$, $df = 8$, $P < 0.0001$; polar, $\chi^2 = 1,160$, $df = 6$, $P < 0.0001$). Cape Petrels and Herald Petrels had very high feeding incidences, whereas Black-winged Petrels, Bulwer's Petrels, Kerguelen Petrels, and Mottled Petrels had especially low feeding incidences.

DISCUSSION

Because species are part of a hierarchical, branching phylogeny, they may share similar traits solely as a result of common ancestry (Felsenstein 1985). Therefore, risks accrue in analyses such as ours (i.e. committing Type I errors) that compare traits of a group of species representing six genera (polar avifauna) with those of a group representing only two genera (tropical avifauna).

However, our treatment of the tropical *Pterodroma* as distinct species was justified for two reasons. First, the results indicated that structurally the two polar *Pterodroma* (Mottled and Kerguelen petrels) were quite similar to the more distantly related polar species (the ful-

TABLE 6. Indices for sexual dimorphism (DI) relative to scaled variances of six morphological characters (SD averaged between PC1 and PC2 values; Fig. 8) among eight tropical petrels and five polar petrels. DIs were calculated as the mean scaled character values (not shown) for lean body mass of females divided by that of males, multiplied by 100. Mean DIs were calculated as the average DI across the six characters. Negative DIs indicate large-scale character values among females compared to males, although negative values were considered as positive for calculation of mean DIs. For sample sizes, F = females, M = males.

Species	Bill length	Bill depth	Tarsus length	Wing span	Wing area	Aspect ratio	Mean DI	Character variance	F	M
Tropical species										
Juan Fernandez Petrel	1.4	1.3	1.3	-0.2	-1.3	1.8	1.2	0.68	82	125
White-necked Petrel	2.4	2.0	0.9	0.6	-2.0	2.7	1.8	0.65	6	8
Tahiti Petrel	1.8	5.0	0.0	-1.1	-1.5	0.0	1.6	0.63	59	82
Kermadec Petrel	1.4	-4.0	-1.4	-1.7	-1.5	-0.9	1.8	0.73	8	4
Phoenix Petrel	2.1	3.6	0.4	-0.3	-0.7	0.0	1.2	0.95	5	14
White-winged Petrel	0.0	2.3	3.0	-1.3	-0.7	0.0	1.2	0.79	57	72
Black-winged Petrel	-0.1	4.2	2.1	0.4	0.2	0.0	1.2	0.61	45	36
Bulwer's Petrel	1.8	5.6	2.5	<0.1	-1.5	2.8	2.4	0.94	23	17
Average (Tropical)	1.4	3.5	1.5	0.7	1.2	1.0	1.6			
Polar species										
Southern Fulmar	2.8	7.8	1.7	-0.1	-5.0	2.0	3.2	0.44	9	12
Antarctic Petrel	<0.1	6.0	0.2	-1.0	-3.8	0.9	2.0	0.59	22	37
Cape Petrel	1.6	6.5	-0.3	-2.5	-2.3	4.0	2.9	1.05	8	7
Snow Petrel	3.4	0.8	3.0	2.4	-0.9	4.0	2.4	0.52	36	44
Blue Petrel	0.9	0.0	0.5	-0.8	-0.8	1.0	0.7	0.29	9	11
Average (Polar)	1.7	4.2	1.1	1.4	2.6	2.4	2.2			
Average (Overall)	1.6	3.9	1.3	1.1	1.9	1.7	1.9			

TABLE 7. Feeding methods used during daylight by petrels in the eastern tropical Pacific and Southern Ocean. Numbers are percent of observations by species for each method of feeding. "Surface seize" includes capture of live prey as well as scavenging. "Feeding incidence" is the proportion of the total number of individuals recorded during at-sea surveys that were feeding.

Species	n	Feeding method					Feeding incidence
		Surface seize	Contact dip/surface plunge	Pursuit dive/pursuit plunge	Aerial pursuit	Piracy	
Tropical species							
Juan Fernandez Petrel	272	22.4	0.0	0.0	76.8	0.0	3.9
White-necked Petrel	6	0.0	0.0	0.0	100.0	0.0	2.9
Tahiti Petrel	41	100.0	0.0	0.0	0.0	0.0	5.7
Kermadec Petrel	8	50.0	0.0	0.0	0.0	50.0	4.2
Phoenix Petrel	8	0.0	75.0	0.0	25.0	0.0	6.2
Herald Petrel	12	8.3	25.0	0.0	66.7	0.0	14.1
White-winged Petrel	51	70.6	23.5	0.0	5.9	0.0	3.3
Black-winged Petrel	36	69.4	30.6	0.0	0.0	0.0	1.7
Bulwer's Petrel	9	88.9	0.0	0.0	0.0	11.1	1.7
Total	441	39.9	7.3	0.0	51.7	1.1	3.5
Polar species							
Southern Fulmar	141	92.9	7.1	0.0	0.0	0.0	2.8
Antarctic Petrel	175	32.0	48.0	18.9	0.0	0.1	2.7
Cape Petrel	703	94.0	6.0	0.0	0.0	0.0	19.8
Kerguelen Petrel	4	0.0	50.0	50.0	0.0	0.0	1.7
Mottled Petrel	3	33.3	0.0	66.7	0.0	0.0	1.3
Snow Petrel	511	7.8	91.8	0.4	0.0	0.0	7.4
Blue Petrel	45	35.6	64.4	0.0	0.0	0.0	2.1
Total	1,582	57.2	40.2	2.5	0.0	0.1	5.6

marine petrels) but quite distinct from the closely related tropical *Pterodroma*. Second, no form of fulmarine petrel inhabits the highly pelagic tropical environment (see Harrison 1983), although *Fulmarus* has radiated from southern polar regions across (but bypassed) tropical oceans to inhabit subarctic regions (i.e. the Northern Fulmar [*Fulmarus glacialis*]). Indeed, the dominance of fulmarine petrels in polar waters of the Southern Ocean (79.1% of all procellariid petrels we recorded there; Table 1) and the nearly complete dominance by *Pterodroma* in tropical oceans (95.7% of all the procellariid petrels we recorded in the ETP), indicate that these taxa have developed distinct traits to inhabit their respective habitats. Similar taxonomic composition also occurs in tropical versus polar avifaunas of the Indian (Stahl et al. 1996) and Atlantic (Harrison 1983) oceans. In summary, the structural differences between tropical versus polar *Pterodroma*, and the absence of fulmarine petrels in pelagic, tropical waters, suggest that the morphological differ-

ences we identified between the two avifaunas are evolved adaptations.

Structural adaptations of polar and tropical avifaunas.—The differences between the tropical and polar avifaunas in the ratio of limb measurements to body mass were independent of differences in fat load, indicating that the differences were structural. Yet, the much heavier fat loads among polar species were, by themselves, a major difference between the two groups. This result is not surprising given that many studies have shown that fat reserves in birds are larger at higher latitudes (see Lima 1986). Lima put forth several explanations for these differences in small species of birds; namely, that in higher latitudes they more often experience harsh weather and, therefore, must be more resilient to periods when they cannot feed effectively. Another possibility is that polar species require thicker fat deposits to maintain body heat (Krebs and Houston 1989). Consistent with this idea, tropical species live in a warm climate and rarely experience weather

conditions severe enough to prevent them from feeding. Furthermore, large fat reserves might encumber tropical species that depend on fast acceleration and maneuverability to feed effectively (see below).

With exception of the Cape Petrel, polar species also had lower variances among morphological characters (i.e. a more consistent body structure among individuals) than did tropical petrels. This difference was affected little by sexual dimorphism, because species differences in degree of sexual dimorphism differed little between avifaunas; nor were these differences correlated with character variances. Higher character variances among tropical species suggest that these species are less specialized than are polar species, possibly because tropical species experience a wider range of environmental conditions (Ainley et al. 1992, 1993). For example, most of the tropical species we studied breed in temperate latitudes where physical factors (e.g. winds) and biological factors (e.g. prey species) are different from those of their tropical wintering areas. In contrast, most of the polar species we studied stay in polar or subpolar latitudes year-round, possibly leading to the development of more specialized adaptations for existence in a given habitat (e.g. pack ice, open water, or the ice edge-boundary; Ainley et al. 1994) where climate and diet vary little with season.

Compared with petrels of polar waters, tropical species had proportionally longer and deeper bills, longer tails, and longer wings with greater surface area. These differences may reflect adaptations to three fundamental environmental differences: (1) food supplies are more patchy and less abundant in tropical waters (Foxton 1956; Ashmole 1963, 1971); (2) prey in the Southern Ocean concentrate near the surface and have low mobility (e.g. krill and small schooling fish), whereas most prey are highly mobile in the tropics (Ashmole 1963, Ainley 1977, Au and Pitman 1986, Ballance et al. 1997); and (3) wind speeds are much higher in the Southern Ocean (Ainley and Boekelheide 1983, van Loon and Rogers 1984, Philander 1989).

The most remarkable morphological difference between the two avifaunas was in wing span and wing area. Species that feed on highly mobile prey should possess larger wings compared with species that feed on less-mobile prey, because larger wing areas increase ma-

neuverability (Ainley and Boekelheide 1983; also see Pennycuick 1989). Larger wing areas also would increase the ability to accelerate when pursuing volant prey (see Pennycuick 1989) such as flying fish (Exocoetidae) and flying squid (*Symplectoteuthis* spp.), which leap from the water into a prolonged, airborne escape mode when pursued by aquatic predators. In addition, with lower wind speeds and less abundant, more dispersed food sources, tropical petrels should benefit from (or require) proportionally longer wings of larger area (i.e. lower wing loading) to use wind efficiently when foraging over large expanses of ocean (Spear and Ainley 1997b). In contrast, polar species should depend less on fast acceleration or mobility and likely would be encumbered by large wings in the high winds characteristic of the Southern Ocean (see Pennycuick 1989).

The larger bill of tropical species also was not surprising, because this feature should improve success when pursuing highly mobile prey. On the other hand, a large bill would be less likely to help polar species when pursuing their more concentrated, less-mobile prey and might be a disadvantage if the energetic cost (through loss of body heat) of having a large, noninsulated extremity was higher than the energy gain if prey became easier to capture.

Species-specific structural adaptations in tropical species.—Morphology of the nine species of tropical petrels conformed well with the taxonomic classification at the generic level. With the exception of the Tahiti Petrel, the *Pterodroma* showed considerable structural overlap but differed from *Bulweria*. Indeed, the marked structural divergence of the Tahiti Petrel from other *Pterodroma* offers support for the idea that this petrel represents a monospecific genus (Mathews 1942, Imber 1985). However, the genus *Pseudobulweria* may not be appropriate for the Tahiti Petrel, because in many ways this petrel is structurally (and behaviorally; see below) as distinct from *Bulweria* as it is from the other seven species of tropical *Pterodroma* that we examined.

The distinctiveness of the Tahiti Petrel from other tropical species resulted from its extremely long tarsus, very robust bill, high aspect ratio, small wing area, short tail, and very small pectoral muscles. These characteristics are probably related to the fact that this species feeds exclusively by scavenging dead squid (Spear and Ainley unpubl. data), in contrast to other tropical pet-

rels that feed mostly by capturing live prey small enough to be swallowed whole. Thus, the robust bill and long tarsus of the Tahiti Petrel are likely to be adaptations for ripping flesh from squid too large to be swallowed whole (the bill for seizing and the long feet for support, either by pushing against the water or against the squid; Spear and Ainley pers. obs.). The high aspect ratio, small wing area (i.e. high wing loading), and short tail of Tahiti Petrels are additional adaptations that allow optimal gliding efficiency over large expanses of ocean (Pennycuik 1989, Spear and Ainley 1997b) while they search for nonactive prey. In contrast, the larger wing area, lower aspect ratio, and larger pectoral muscles of other tropical species are probably related to a compromise between adaptations for optimal flight efficiency versus fast acceleration when chasing volant prey (most larger *Pterodroma*), or to maneuverability (most small *Pterodroma* and *Bulweria*) for feeding on nonvolant but mobile prey (Ainley and Spear unpubl. data, Harrison et al. 1983).

The very long tail and large wing area of Bulwer's Petrels and Black-winged Petrels probably are adaptations for maneuvering (Pennycuik 1989) to catch myctophids, which are highly mobile (albeit nonvolant) mesopelagic fish that perform vertical migrations to the ocean surface at night. Indeed, Bulwer's Petrels and Black-winged Petrels were the only tropical species (other than the Tahiti Petrel and Kermadec Petrel; see above and below, respectively) not observed in pursuit of volant prey. This difference possibly is related to the small pectoral mass of the Black-winged Petrel (pectorals of Bulwer's Petrel not measured). Compared with other tropical species, the Bulwer's and Black-winged petrels also had the lowest incidences of feeding during our daytime observations. If we assume that feeding frequency during a given 24-h period is approximately equal among the tropical petrels, this result offers evidence for crepuscular or nocturnal feeding. Nocturnal feeding by the Bulwer's Petrel has been indicated from prey samples taken on the Hawaiian Islands (Harrison et al. 1983).

Although three morphological characters (aspect ratio, wing area, and fat load) were similar when compared between Black-winged and White-winged petrels, i.e. the two species of "Cookilaria" (see Warham 1996) that we studied, these species differed in six other features: deeper bill, longer tarsus, longer tail, and longer

wing span of the Black-winged Petrel and the longer bill and larger pectoral muscles of the White-winged Petrel. Although the feeding methods used were mostly similar, only the White-winged Petrel pursued volant prey above predatory fish, a habit that could account for the differences in bill structure and pectoral mass. In addition, the feeding frequency of the White-winged Petrel during daylight was twice as high as that of the Black-winged Petrel, suggesting differences in diurnal versus nocturnal feeding.

We suspect that the low aspect ratio, large pectoral muscles, and extremely short tail of the Kermadec Petrel are adaptations related to mimicry of skuas and jaegers that pirate petrel hosts (Spear and Ainley 1993). Although one might expect an avian pirate to have a large tail to improve maneuverability (as in Long-tailed Jaegers [*Stercorarius longicaudus*] and Parasitic Jaegers [*S. parasiticus*]), Kermadec Petrels mimic subadults and nonbreeding adults of the large Pomarine Jaeger (*S. pomarinus*) and South Polar Skua (*Catharacta maccormicki*). The latter have very short tails and rely on fast acceleration to surprise their avian hosts (Spear and Ainley 1993). Hence, the unique morphological features of the Kermadec Petrel, compared with other *Pterodroma*, are consistent with those expected for a pirate-mimic of this type.

Species-specific structural adaptations in polar species.—Compared with tropical species, the overlap in morphology was much lower among polar species. This was consistent with the monogeneric status (five of seven species) and low character variances. Three species, Southern Fulmar, Snow Petrel, and Mottled Petrel, were distinct from each other and from each of the four other species, and, with exception of the Cape Petrel and Blue Petrel, the latter four also overlapped little in morphology.

The Snow Petrel was the most distinct polar species examined, having a larger wing area, lower aspect ratio, shorter and narrower bill, and longer tail. This species' completely white plumage is also distinct. The wing and tail characteristics and white plumage likely are related to this petrel's exclusive use of prey that concentrate around the edges of ice, including icebergs floating in the open ocean, as well as small leads within the pack ice (Ainley and Boekelheide 1983; Griffiths 1983; Ainley et al. 1984, 1992). Exploiting prey in these habitats requires more proficient maneuvering than found in other po-

lar species (including the Antarctic Petrel), which feed in less-confining situations.

Like the Snow Petrel, the Antarctic Petrel also occurs primarily in ice habitat (Ainley et al. 1984, 1992). In contrast to the Snow Petrel (and other polar species), however, the Antarctic Petrel is distinct in having a very small wing area and short tail, short wings, and a high aspect ratio, indicating ecological divergence. These morphological characteristics are advantageous for swift flight in very strong winds and for diving in pursuit of prey (see Spear and Ainley 1997a), a feeding method frequently used by this species but, with the exception of Kerguelen Petrels and Mottled Petrels (see below), rarely used by other species of polar petrels.

Imber (1985) suggested that the Kerguelen Petrel was a highly specialized species, an idea supported by the small amount of character overlap with other polar species and low character variance. The Mottled Petrel also had very low character variance and no character overlap, yet the morphological characteristics of both species were mostly intermediate within the polar avifauna. The available evidence indicates that both species feed nocturnally (Harper 1987), an idea supported by diet (Ainley et al. 1992) and the very low feeding incidence. Our daylight observations also indicated that, with the possible exception of the Antarctic Petrel, these species rely to a larger extent on pursuit diving than do the other polar species.

The Cape Petrel's high character variance indicates that it is a generalist that is capable of exploiting a wide range of habitats and prey types. Consistent with this idea, Cape Petrels feed extensively on krill above the continental shelf (Heinemann et al. 1989; see also Greene 1986), but also feed over pelagic waters, mostly on squid and fish (Ainley et al. 1984, 1992). Furthermore, this species' diet was among the most variable of the polar avifauna. Although these petrels fed mostly by surface seizing (this study), they also fed by surface plunging (this study) and pursuit diving (Warham 1996). Among polar species, the Cape Petrel also had by far the highest feeding incidence during our daytime observations, yet it also feeds at night (Harper 1987). Finally, the Cape Petrel is one of only two polar species we studied that disperses extensively to temperate habitats, e.g. the Peru and Benguela currents (Murphy 1936, Abrams and Griffiths 1981).

The Southern Fulmar was the second species for which an appreciable segment of the population disperses north into more temperate latitudes during the nonbreeding season (Murphy 1936, Abrams and Griffiths 1981). Unlike the Cape Petrel, however, character variance of the fulmar was low and the morphological structure was distinct, mostly as a result of the fulmar's very long, deep bill. Differences in diet between Southern Fulmars and the other polar petrels we studied might explain the large bill. These differences include: (1) the greater proportion of squid in the fulmar's diet, and (2) the significantly larger size of prey eaten by the fulmar compared with prey eaten by the other polar petrels (Ainley et al. 1984, 1992).

Conclusion.—We have identified several morphological differences between the tropical and polar avifaunas that appear to be independent of sexual differences or ancestral relationships. The most consistent and marked differences are in the structure of the wings and in fat loads, both of which are directly related to adaptations to physical factors such as wind regimes and climate. Morphological differences within avifaunas and within-species character variances indicated that the tropical Pacific is used by a more generalist, migratory group of petrels, whereas the polar waters of the Southern Ocean are used by a more specialized, resident group.

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APPENDIX. Summary statistics ($\bar{x} \pm SE$, with n in parentheses) for morphological variables and fat scores of 16 species of petrels of the tropical Pacific and Southern Ocean. JF = Juan Fernandez Petrel, WN = White-necked Petrel, TA = Tahiti Petrel, KE = Kermadec Petrel, PH = Phoenix Petrel, HE = Herald/Henderson petrel, WW = White-winged Petrel, BU = Bulwer's Petrel, SF = Southern Fulmar, AP = Antarctic Petrel, CA = Cape Petrel, MO = Mottled Petrel, KG = Kerguelen Petrel, SN = Snow Petrel, and BL = Blue Petrel. All measurements of Cape Petrels were of the nominate race (*Daption capense capense*; see Harrison 1983). Measurements of Herald/Henderson petrels were equally divided between the two species; those of White-winged Petrels were nominate race (5%), and smaller race (95%) (*Pterodroma leucoptera caledonica*; see Imber and Jenkins (1981). Body mass includes the mass of subcutaneous and mesenteric fat.

Species	Fresh mass (g)	Lean mass (g)	Wing span (mm)	Wing area (cm ²)	Tail length (mm)	Bill length (mm)	Bill depth (mm)	Tarsus length (mm)	Aspect ratio	Fat score
Tropical species										
JF	428 ± 3.3 (207)	425 ± 3.2	1,067 ± 1.7 (149)	878 ± 3.8 (119)	136 ± 1.0 (47)	38.2 ± 0.1 (146)	11.4 ± 0.01 (138)	39.8 ± 0.1 (149)	10.9 ± 0.03 (119)	0.4 ± 0.04 (207)
WN	410 ± 7.6 (14)	400 ± 7.3	1,045 ± 5.9 (10)	816 ± 16.9 (8)	125 ± 1.6 (6)	35.6 ± 0.3 (10)	10.9 ± 0.14 (5)	39.0 ± 0.4 (10)	11.1 ± 0.13 (8)	1.3 ± 0.26 (13)
TA	409 ± 3.2 (141)	384 ± 3.1	1,052 ± 2.3 (97)	793 ± 5.1 (80)	115 ± 0.9 (32)	36.5 ± 0.1 (97)	11.4 ± 0.06 (97)	47.8 ± 0.1 (98)	11.8 ± 0.04 (80)	2.4 ± 0.08 (140)
KE	369 ± 9.8 (12)	360 ± 9.4	1,010 ± 3.5 (12)	795 ± 18.0 (12)	105 ± 1.2 (7)	30.3 ± 0.3 (10)	8.8 ± 0.09 (5)	39.6 ± 0.3 (10)	10.6 ± 0.11 (12)	1.4 ± 0.19 (12)
PH	284 ± 7.5 (19)	270 ± 7.3	948 ± 5.5 (17)	690 ± 9.2 (17)	114 ± 1.3 (7)	28.1 ± 0.2 (17)	9.0 ± 0.14 (17)	34.0 ± 0.2 (17)	11.2 ± 0.07 (17)	2.1 ± 0.24 (19)
HE	277 ± 6.9 (13)	265 ± 6.8	932 ± 8.3 (4)	640 ± 16.3 (4)	108 ± 2.2 (4)	27.3 ± 0.3 (4)	8.1 ± 0.09 (3)	33.7 ± 0.5 (4)	11.2 ± 0.03 (4)	1.6 ± 0.39 (13)
WW	159 ± 1.3 (129)	155 ± 1.3	752 ± 1.6 (90)	474 ± 3.2 (65)	94 ± 1.0 (17)	25.9 ± 0.1 (89)	7.0 ± 0.04 (85)	29.6 ± 0.1 (88)	10.1 ± 0.04 (65)	1.3 ± 0.06 (129)
BW	153 ± 1.3 (81)	149 ± 1.3	756 ± 1.8 (61)	474 ± 3.2 (58)	102 ± 0.8 (27)	24.5 ± 0.1 (61)	7.3 ± 0.04 (58)	29.9 ± 0.1 (61)	10.2 ± 0.05 (58)	1.5 ± 0.09 (81)
BU	91 ± 1.8 (40)	84 ± 1.7	654 ± 2.9 (29)	400 ± 3.4 (28)	104 ± 1.7 (6)	21.5 ± 0.2 (29)	6.1 ± 0.07 (28)	26.4 ± 0.2 (28)	10.8 ± 0.13 (28)	2.5 ± 0.19 (40)
Polar species										
SF	784 ± 18.9 (21)	724 ± 16.9	1,065 ± 9.3 (15)	1,014 ± 17.7 (15)	132 ± 2.0 (8)	45.2 ± 0.5 (15)	13.0 ± 0.23 (15)	51.7 ± 0.5 (15)	10.3 ± 0.10 (15)	3.0 ± 0.32 (21)
AP	676 ± 10.1 (59)	625 ± 10.5	1,041 ± 3.6 (58)	832 ± 7.7 (27)	119 ± 1.7 (23)	36.8 ± 0.2 (58)	10.8 ± 0.11 (56)	44.8 ± 0.2 (58)	11.3 ± 0.11 (27)	3.2 ± 0.15 (59)
CA	441 ± 16.2 (15)	406 ± 10.9	908 ± 12.0 (15)	670 ± 13.0 (10)	105 ± 4.0 (7)	31.0 ± 0.6 (15)	9.0 ± 0.13 (15)	45.8 ± 0.2 (15)	10.0 ± 0.29 (10)	3.7 ± 0.17 (15)
MO	360 ± 5.4 (3)	308 ± 5.3	855 ± 11.4 (3)	593 ± 7.3 (3)	100 ± 0.9 (3)	27.4 ± 0.1 (3)	8.4 ± 0.07 (3)	34.7 ± 0.6 (3)	10.5 ± 0.09 (3)	4.0 ± 0.00 (3)
KG	337 ± 5.5 (5)	311 ± 5.4	875 ± 7.1 (5)	574 ± 8.9 (5)	107 ± 2.0 (5)	27.0 ± 0.1 (5)	8.8 ± 0.11 (5)	37.9 ± 0.3 (5)	11.8 ± 0.10 (5)	3.0 ± 0.00 (5)
SN	320 ± 5.1 (80)	284 ± 5.0	824 ± 4.2 (80)	644 ± 3.2 (33)	121 ± 1.4 (32)	20.8 ± 0.2 (80)	8.2 ± 0.11 (77)	34.1 ± 0.2 (80)	9.6 ± 0.09 (33)	3.9 ± 0.04 (80)
BL	204 ± 4.2 (20)	117 ± 3.2	710 ± 3.4 (20)	426 ± 3.3 (15)	92 ± 0.9 (14)	25.9 ± 0.2 (20)	7.4 ± 0.12 (18)	33.3 ± 0.2 (20)	10.0 ± 0.12 (15)	3.3 ± 0.25 (20)