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DIFFERENCES AMONG DARK-RUMPED PETREL (*Pterodroma phaeopygia*) POPULATIONS WITHIN THE GALAPAGOS ARCHIPELAGO [1]

By R. J. TOMKINS and B. J. MILNE

ABSTRACT

Differences in the time of onset of breeding, morphology, egg size, plumage and vocalisations of Dark-rumped Petrels (*Pterodroma phaeopygia phaeopygia*) were investigated on four islands in the Galapagos. Comparisons were made with *P. p. sandwichensis* in Hawaii. In Galapagos, breeding cycles differed among islands, and on San Cristobal there were two populations that bred at different times. On Floreana, colonies at different altitudes bred at different times. Eggs were laid on Santiago over four consecutive months; on Santa Cruz the egg-laying period was shorter.

Analyses of morphological measurements and notional volume separated Galapagos Dark-rumped Petrels into three groups. Birds on Santa Cruz and those breeding in the middle of the year on San Cristobal were the smallest; birds on Santiago and those breeding at the end of the year on San Cristobal were of intermediate size; and those on Floreana were the largest. There was a similar size trend in the breadth and volume of eggs. No relationship was found between variable plumage patterns on head and chest or between plumage and island populations.

Evidence is presented that supports sexual dimorphism in vocalisations, and it is suggested that males make Sweet calls and females make Coarse calls. There were statistically significant interisland differences among Sweet calls and among Coarse calls. Dialects probably exist within the archipelago. Calls had either one or two introductory syllables. When present, the second introductory syllable was very similar to the single introductory syllable, and these may serve the same function. Discriminant analysis of Sweet calls correctly classified 82.2% of these into island of origin. A similar analysis of morphology correctly classified 58.6% of birds from five populations. A theoretical combination of these two analyses indicates a potential classification rate of 92.6%. Although there are differences among Galapagos populations, there is not yet sufficient evidence to warrant subspecific status.

Vocalisations of the Hawaiian birds were quite different from those in Galapagos, and Galapagos birds were bigger. Dark-rumped Petrels in Galapagos and Hawaii might be more distant taxonomically than currently recognised and they may be different species.

1 Contribution Number 405 of the Charles Darwin Foundation for the Galapagos

INTRODUCTION

Dark-rumped Petrels (*Pterodroma phaeopygia*) breed on the Galapagos (*P.p. phaeopgyia*) and Hawaiian (*P. p. sandwichensis*) archipelagos and are endangered at both locations (King 1981). They are members of the *P. hasitata* superspecies of medium-sized gadfly petrels. This group comprises five to eight low-latitude, dichromatic forms which are similar in colour, size, behaviour and breeding habitat (Murphy & Mowbray 1951, Palmer 1962, Jouanin & Mougin 1979, Warren King, pers. comm.). The calls differ among these forms. Imber (1985) recently included Dark-rumped Petrels in the subgenus *Hallstroma*, and Meredith[2] included them in the *P. neglecta* group.

In Galapagos (Fig. 1), petrels breed on four islands less than 170 km apart. This study includes data from four adjacent colonies on Isla Santa Cruz, nine widespread colonies on Isla Santiago, four widespread colonies on Isla San Cristobal, and two adjacent and one distant colony on Isla Floreana. Here, we regard a colony as an aggregation of burrows in an area of variable size, sometimes as large as 200 m by 300 m. Not all nests in any colony were monitored, nor were all colonies on any island found. Distances between colonies varied from 300 m to 5 km. Local residents are sure that petrels breed on Sierra Negra, Isla Isabela (A. Tupiza, pers. comm.), although nests have not been reported. Petrels have also been seen and heard on other volcanoes on Isabela (Tomkins 1980[3], 1985). Dark-rumped Petrels are pelagic feeders, dispersing to sea after breeding (Harris 1970). At present they breed mostly in the wet and cool zones of the highlands, but this has not always been so, at least on Santa Cruz (Harris 1970). They are annual breeders, and do not replace their single egg if it is damaged or lost. Optimistic estimates of the Galapagos population were up to 100 000 pairs (Baker[4], Duffy 1984, Harris 1984); however, results from recent investigations imply that 7500 breeding pairs are more likely (Tomkins[3]; Cruz & Cruz[5]).

On all breeding islands in Galapagos, Dark-rumped Petrels return to colonies only at night. During this study they were almost silent on their return and for most of the night, but began aerial calling about three hours before sunrise (about 0600 h). However, this pattern might not be typical of all islands, as there are reports that birds began to call shortly after sunset and continued until dawn (Robert I. Bowman, pers. comm., F. and J. Cruz, pers. comm.). The birds call while circling the colony, often during high-speed chases (Fig. 2), and while flying from the colony out to sea. As the number of birds in the air increases shortly before sunrise, calling reaches a maximum. Some birds then return to their burrows, but most fly to sea.

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[2] MEREDITH, C. 1985. The vertebrate fossil fauna of Norfolk Island, and the phylogeny of the genus *Pterodroma*. Unpubl. Ph.D. thesis, Monash University, Melbourne, Australia. 255 pp.

[3] TOMKINS, R.J. 1980. A study of the conservation of the Dark-rumped Petrel (*Pterodroma phaeopygia*): considered to be an endangered species in the Galapagos. Unpubl. report, Charles Darwin Research Station, Galapagos. 74 pp.

[4] BAKER, A.R. 1980. Breeding distribution and population size of the Dark-rumped Petrel (*Pterodroma phaeopygia*) on Santa Cruz Island, Galapagos. Unpubl. report, Charles Darwin Research Station, Galapagos. 78 pp.

[5] CRUZ, F.; CRUZ, J. 1985. The Dark-rumped Petrel conservation project. Unpubl. annual report. Charles Darwin Research Station, Galapagos. 17 pp.

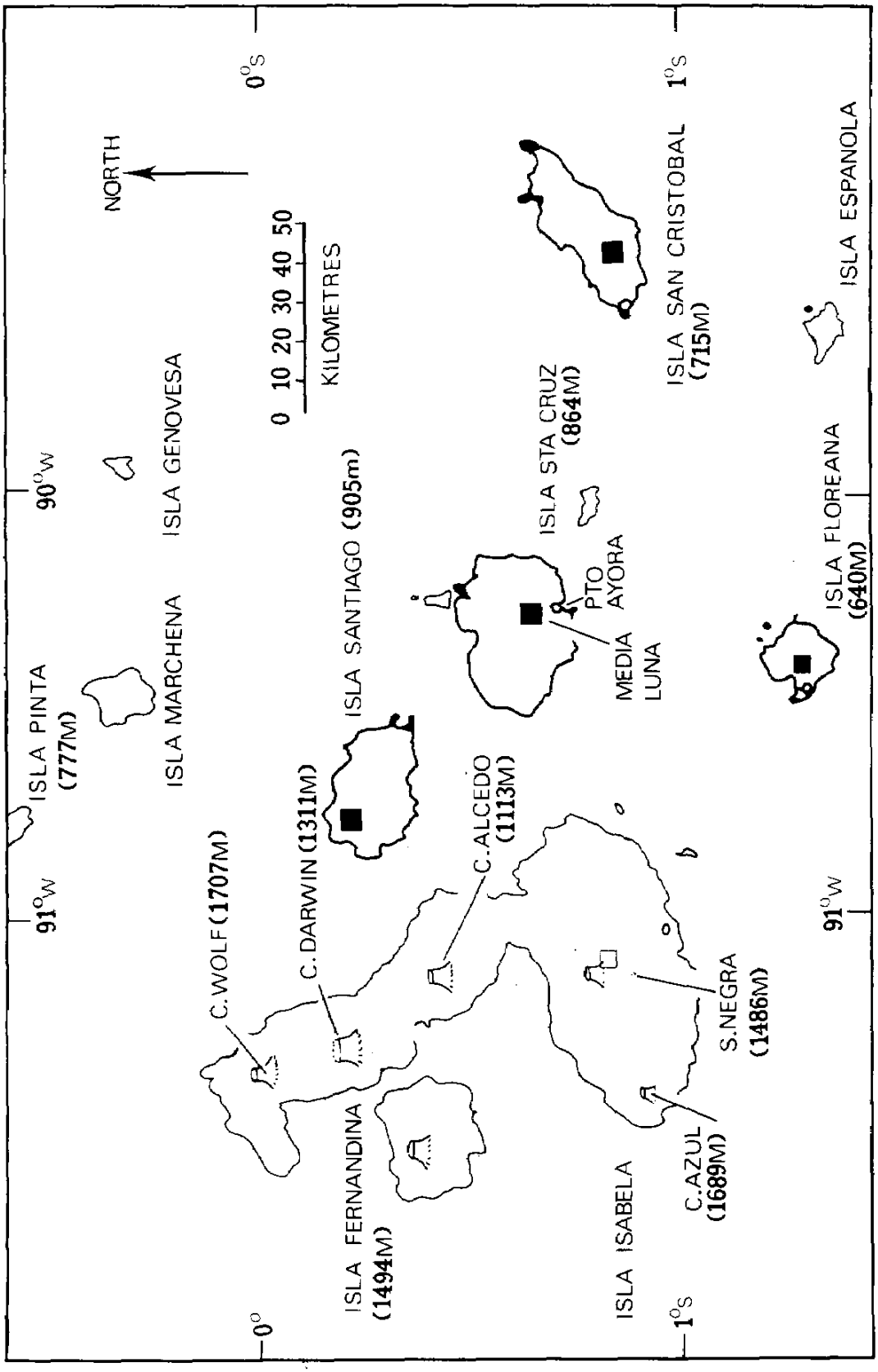

FIGURE 1 — Breeding places of Dark-rumped Petrels on the Galapagos Islands (■). It is almost certain that they breed on Cerro Negra, Isla Isabela,(□) but their burrows have not yet been found there

FIGURE 2 — Dark-rumped Petrels call loudly while circling over colonies before dawn. Different calls are ascribed to males and females

Galapagos Dark-rumped Petrels use three flight calls frequently (Tomkins, in prep.): a short 3 – 5 syllable call (possibly used for identification); a similar but longer call of 6 – 20 + syllables (possibly used in aggressive or defensive situations; Fig. 3); and a single-syllable call (possibly used in conditions of extreme stress; none was analysed). There are two unmistakable forms of the short and long calls. One, which we term the Sweet call, is sweet and pleasant to the ear; the other, termed Coarse, is coarse and grating.

Harris (1970) studied general aspects of this species on Santa Cruz, and Tomkins (1980[3], 1985) studied their breeding success and predators on all four islands. More recently Coulter *et al*[6] investigated petrel predators on

[6] COULTER, M.C.; CRUZ, F.; BEACH, T. 1982. The biology and conservation of the Dark-rumped Petrel, *Pterodrama phaeopygia*, on Floreana Island, Galapagos, Ecuador. Unpubl. report, Charles Darwin Research Station, Galapagos. 33 pp.

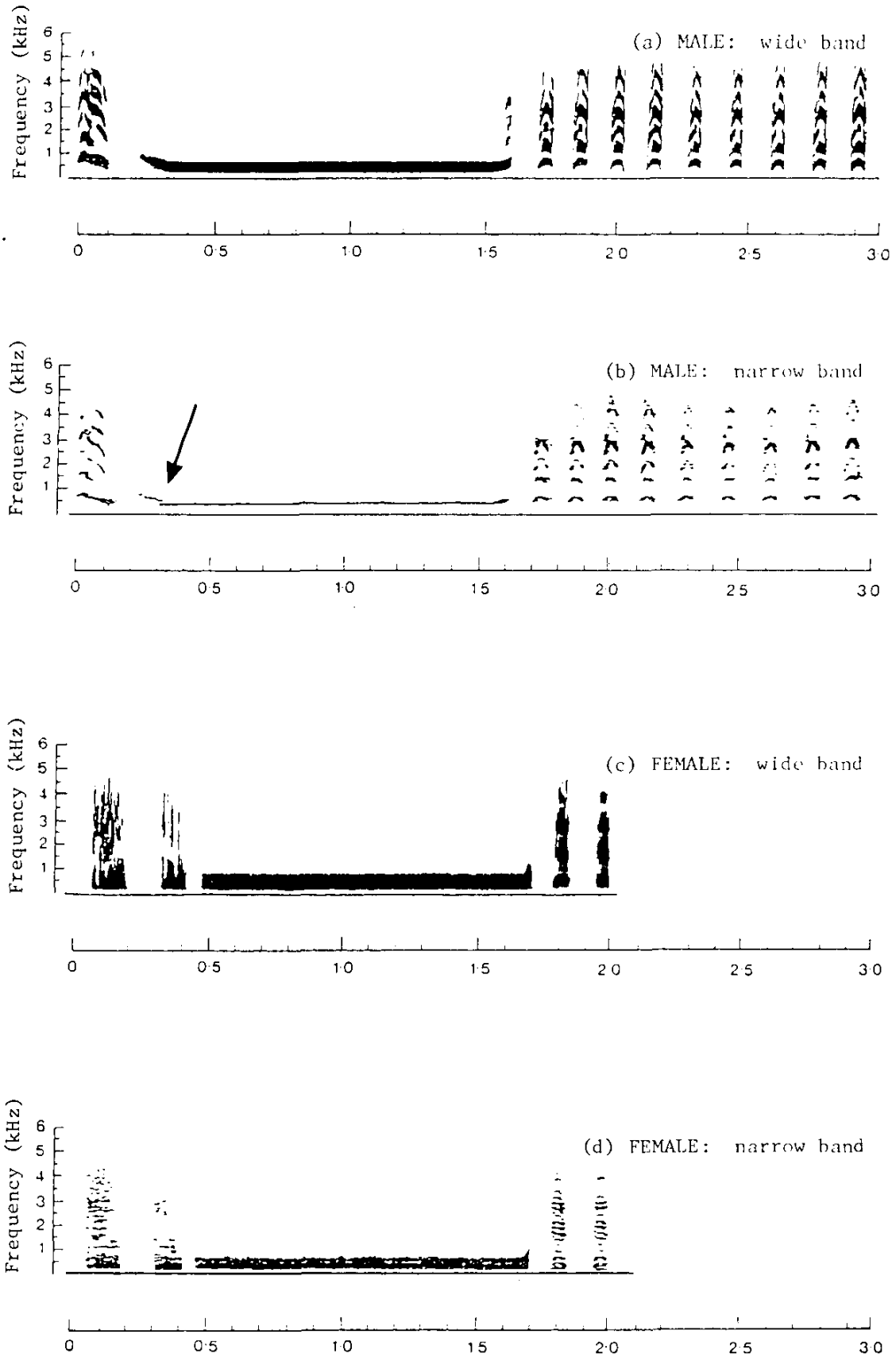

FIGURE 3 — Two of the three common flight calls made by Dark-rumped Petrels. A rare overlap of second and third syllables is arrowed.

Floreana. Cruz & Cruz (1987) studied the diet and breeding phenology of these birds and control of their predators, mainly on Floreana. The Galapagos National Parks Service (SPNG) and the Charles Darwin Research Station (CDRS) are currently monitoring breeding success and controlling predators. Simons (1985) investigated many aspects of this species on the Hawaiian islands.

Over the years, studies have revealed differences in size, breeding phenology, and plumage between specific members of the order Procellariiformes at different locations, but these studies have rarely incorporated vocalisations. It is difficult to provide quantitative analyses of the vocalisations of nocturnal petrels. Several workers have described such calls phonetically (Oliver 1955, Warham 1956, 1979, Wingate 1964, Cramp & Simmons 1977, Imber 1985, Simons 1985) and have often provided sonagrams of "typical" calls, e.g. Brooke (1986). These two tools can only detect gross interpopulation differences. Ainley (1980) quantified some features of sonagrams for comparative studies of Leach's Storm Petrels (*Oceanodroma leucorhoa*), as did James & Robertson (1986) when discussing the usefulness of vocalisations in petrel systematics. We have examined less obvious and more detailed interpopulation differences than did Ainley or James & Robertson.

In this paper we investigate the existence of consistent interisland differences among groups of birds breeding on four islands in Galapagos, by comparing their breeding phenology, morphology, egg size, plumage and vocalisations. Comparisons are made with the Hawaiian subspecies. We discuss possible causes of the differences that were found.

METHODS

Breeding phenology

Burrows on each island were numbered and monitored individually; 232 known breeding attempts in 444 burrows were recorded (Tomkins 1985). Colonies on Santa Cruz were visited 31 times in 1978 and 1979, and the colonies on other breeding islands were visited 4 – 5 times, mostly in 1979. Adults and large chicks were banded with numbered metal bands from the British Museum. We estimated the age of eggs by comparing their weights with eggs of known age, by their cleanliness, and by the parents' attendance at the burrow. We estimated the age of chicks by comparison with known-age chicks, and by the colour and type of their down. Thus, we established a breeding timetable for each nest and verified or adjusted it based on information from subsequent visits. We compared sample distributions of laying dates using ANOVA and t-tests.

In the absence of a standard statistical procedure, we tested whether the distribution of laying dates for San Cristobal was bimodal or uniform, using a method suggested by Dr R. C. Griffiths, Mathematics Department, Monash University. The hypothesis that the sample distribution was a mixture of two distinct temporally separated samples was tested against the null hypothesis that egg laying was uniformly random (Fig. 4). The test is done by first sorting the dates. Any date can then be arbitrarily chosen to separate the sample distribution into two subgroups; the date that optimally separates the sample into two distinct subgroups is defined as the one which minimises the sum

of the variances of the two subgroups. The minimum variance sum statistic derived in this way may then be compared with similar statistics computed from randomly generated uniform distributions.

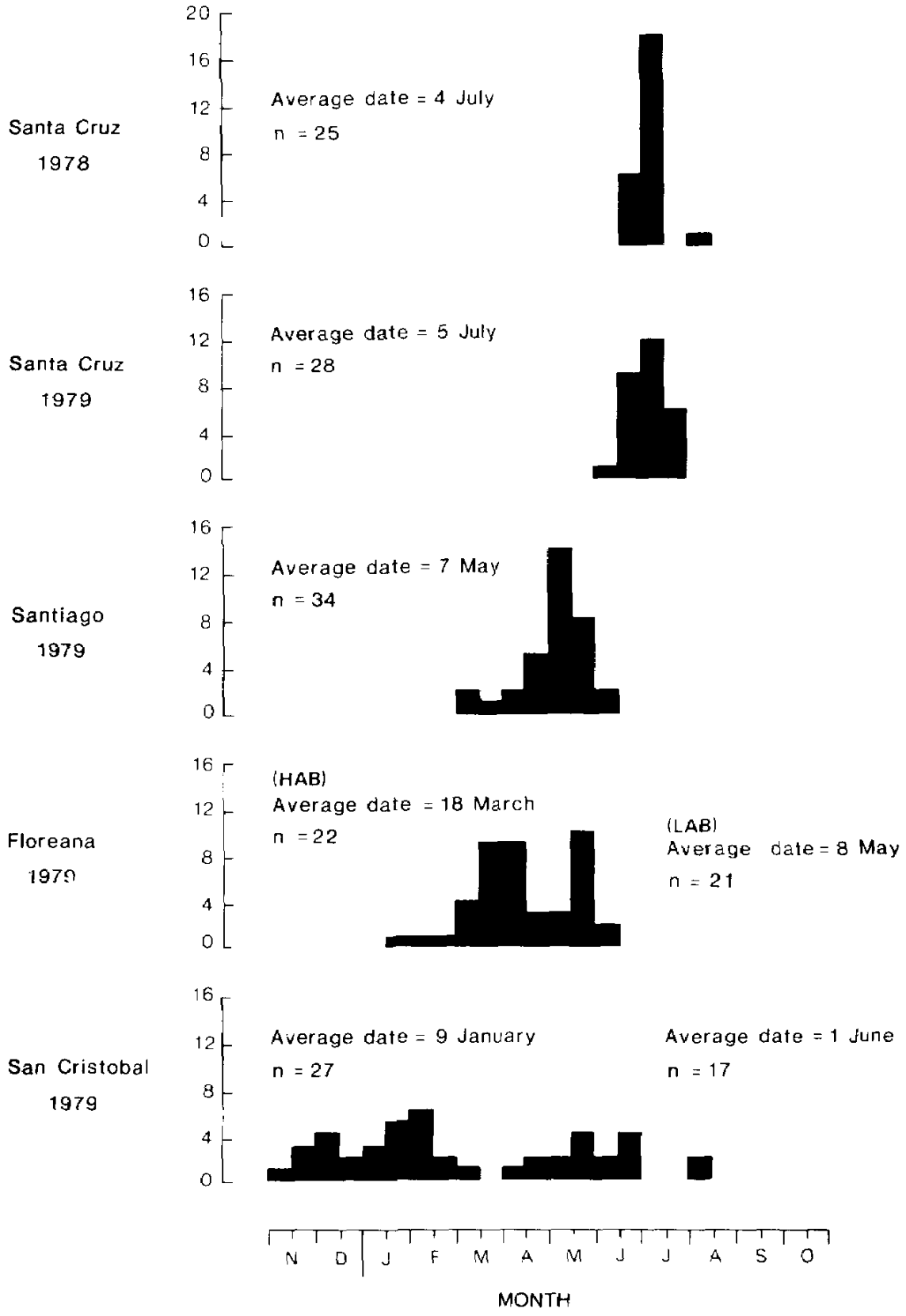

FIGURE 4 — Estimated laying dates among and within islands.

Morphology and weight

RJT caught all birds in burrows by day, banded them, and measured them with calipers and a rule. Bill depth was measured (± 0.1 mm) at the shallowest part, anterior to the nares. The exposed culmen (for live Galapagos birds and Hawaiian museum specimens) was measured (± 0.1 mm) as the maximum distance from the junction of skin and upper mandible on the forehead to the most distant part of the unguis, i.e. to the curve, not the bill tip. Although the difference between these two measurements of length in Dark-rumped Petrels and similar species is less than 0.3% (Tomkins, unpubl. data), the advantage of the maximum-distance measurement over the usual culmen length measurement (Baldwin *et al.* 1931) in Procellariiformes is that it is less influenced by wear (Tomkins 1984). There was great variation in the size of the latericorn plate on the sides of birds' bills, but as it was difficult to measure this plate accurately on live birds, the significance of this variation could not be investigated. Chords (± 1 mm) of flattened wings were measured, as were lengths of the central tail feathers (± 1 mm), tarsus, and middle toe excluding claw (± 0.1 mm). A notional index of the volume of each bird was calculated by multiplying together the six mensural values and taking the square root of the product; thus, it may be considered as an aggregative variable. Galapagos birds were weighed (± 2 g) in a bag with a Pesola 1 kg spring balance. Consecutive weight readings taken a few weeks apart on the same individual varied by up to 20% (Tomkins, unpubl. data). This great fluctuation is common in Procellariiformes (Imber 1976, Dunnet 1985). Although we consider weight to be unreliable for taxonomy, we have included weights in preliminary analyses to allow future workers to make comparisons with similar species. We ascertained the sex of only 19 birds (from different islands), by examination of cloacae and dissecting dead birds. This was an inadequate sample size to investigate sexual dimorphism.

Based on differences in altitude and breeding phenology, data for the three colonies on Floreana were condensed to two groups, Low-Altitude-Breeders (LAB) and High-Altitude-Breeders (HAB). On San Cristobal egg laying occurred intermittently throughout a ten month period in each of the four colonies. There did not appear to be any association between colonies and laying dates, and following persuasive evidence of bimodality (see Results), data were separated into two groups, End-Of-Year (EOY) breeders and Middle-Of-Year (MOY) breeders. The populations on Santa Cruz and Santiago were each considered to be homogeneous.

One-way ANOVA was applied to the six mensural variables, the derived notional volume, and weight, with population as the classification factor. Following these analyses, the Floreana LAB and HAB samples were amalgamated. Discriminant analysis was then used to separate the five breeding groups, with five mensural variables as predictors.

Measurements of the mensural variables from 11 birds of the Hawaiian subspecies were compared with those from the combined Galapagos sample, using t-tests.

Eggs

Eggs were weighed, and their length and breadth measured (± 0.1 mm) with vernier calipers. A notional index of their volume was obtained by

multiplying length by the square of the breadth. One-way ANOVA was applied to lengths, breadths and volumes. In these analyses, data for the three Floreana colonies were pooled, as also were the data for the four San Cristobal colonies. The analyses therefore tested for differences among islands. We used Student's t-tests to compare the dimensions of eggs from Hawaii (summary data extracted from Simons 1985) and Galapagos.

Plumage

The variable patterns of black and white on the forehead and collar (neck and chest) were scored on a scale of 1 – 10. A very white forehead scored 1, and a very black or heavily speckled forehead scored 10 (Fig. 5). A clean-sided, all-white neck scored 1, and a neck that was very uneven or had black bars across it scored 10 (Fig. 6). Intermediate patterns were given correspondingly intermediate scores. Although aged and worn black feathers were slightly paler than when new, wear did not affect plumage patterns. Mild body and facial moult occurred throughout the breeding cycle; this moult lessened the intensity of black markings but did not alter the overall pattern. Large chicks also have variable forehead and collar patterns, but chicks were not included in these analyses. Statistical tests similar to those for the morphological measurements were applied to the forehead and collar scores, which we treated as interval-level quantities.

Vocalisations

Recordings were made at night at breeding colonies on the four islands with a Nagra III tape recorder and a Dan Gibson parabolic reflector with omnidirectional microphone. These recordings were made on 31 March 1979 on Floreana, 19 May 1979 on Santiago, 20 June and 10 July 1979 on Santa Cruz, and 4 April 1979 on San Cristobal, that is, during egg laying for all islands except San Cristobal, where EOY chicks were about 7 weeks old and MOY birds had just begun to lay. Simons (1985) showed that similar numbers of breeding and non-breeding birds were in the colony during the egg laying period, and we assume that the attendance pattern was similar in Galapagos. Thus we probably recorded calls of both breeding and non-breeding birds.

Based on sound alone, calls were first classified into Sweet or Coarse. Wide- and narrow-band sonagrams of the 320 clearest calls then were prepared with a Kay Elemetrics sonagraph (110 calls from Santa Cruz, 60 from San Cristobal, 100 from Santiago and 50 from Floreana). Some sonagrams were incomplete because the call faded as the bird flew away from the microphone. For other sonagrams, a number of birds calling at the same time prevented some measurements from being accurately deciphered. The difference in clarity between the sonagrams of Sweet and Coarse calls was outstanding. Unusual calls (highly varied and atypical, or possibly Doppler shifted) were omitted from our analyses.

Each call was divided into syllables, and parameters of these syllables were measured (Fig. 7). The number of syllables in both short and long calls varied. Each had either one introductory syllable (called One Of One OOO) or two introductory syllables (First Of Two FOT, Second Of Two SOT), before a protracted syllable called a DRONE. A short, small increase in frequency (UPSWEEP) was seen at the end of each DRONE.

FIGURE 5 — Method of scoring forehead patterns, from palest (1) to darkest (10, not shown)

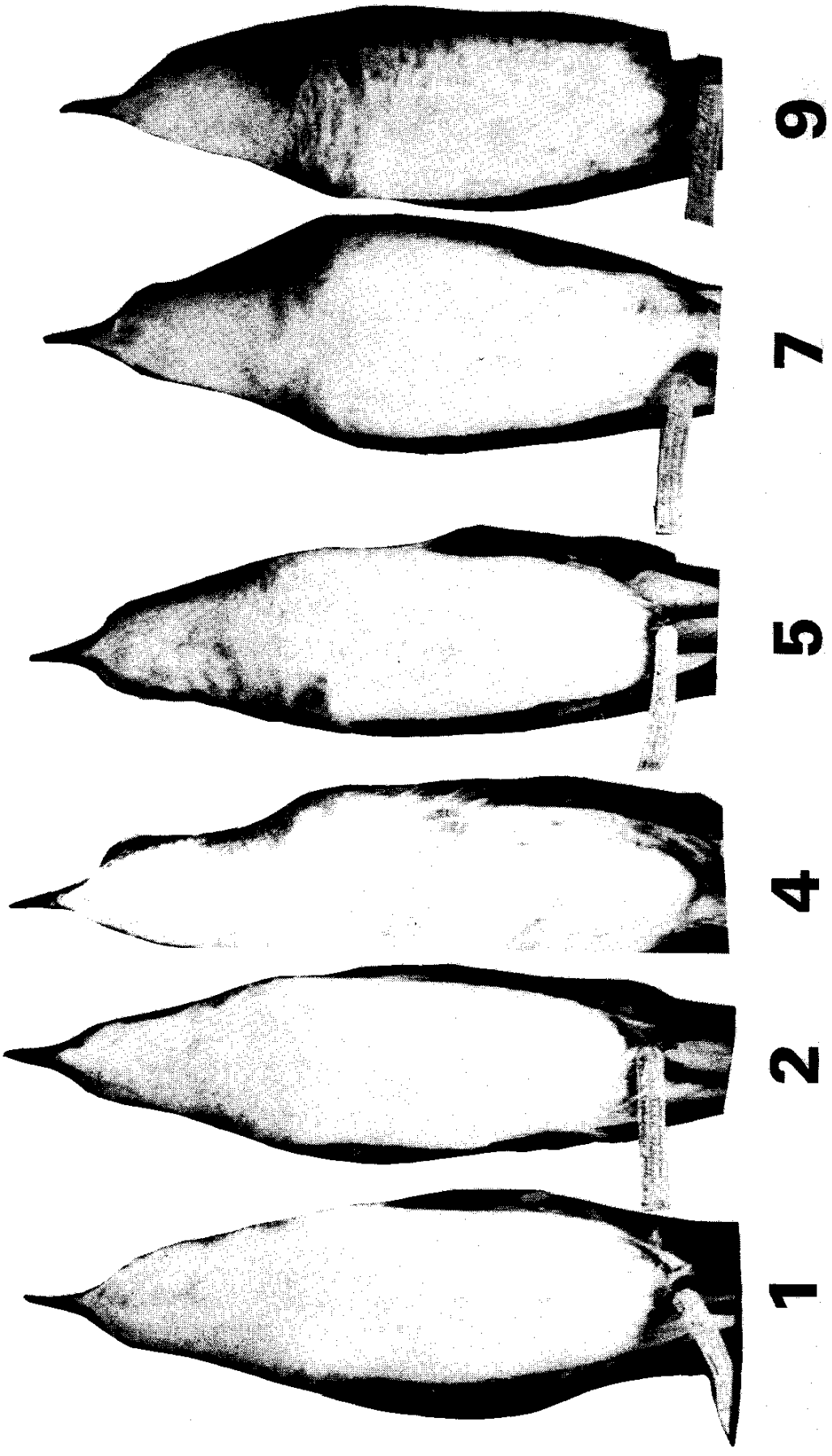

FIGURE 6 — Method of scoring extent of collar. No collar or a slight collar scored 1; collars extending in an almost solid line across the chest scored 10 (not shown)

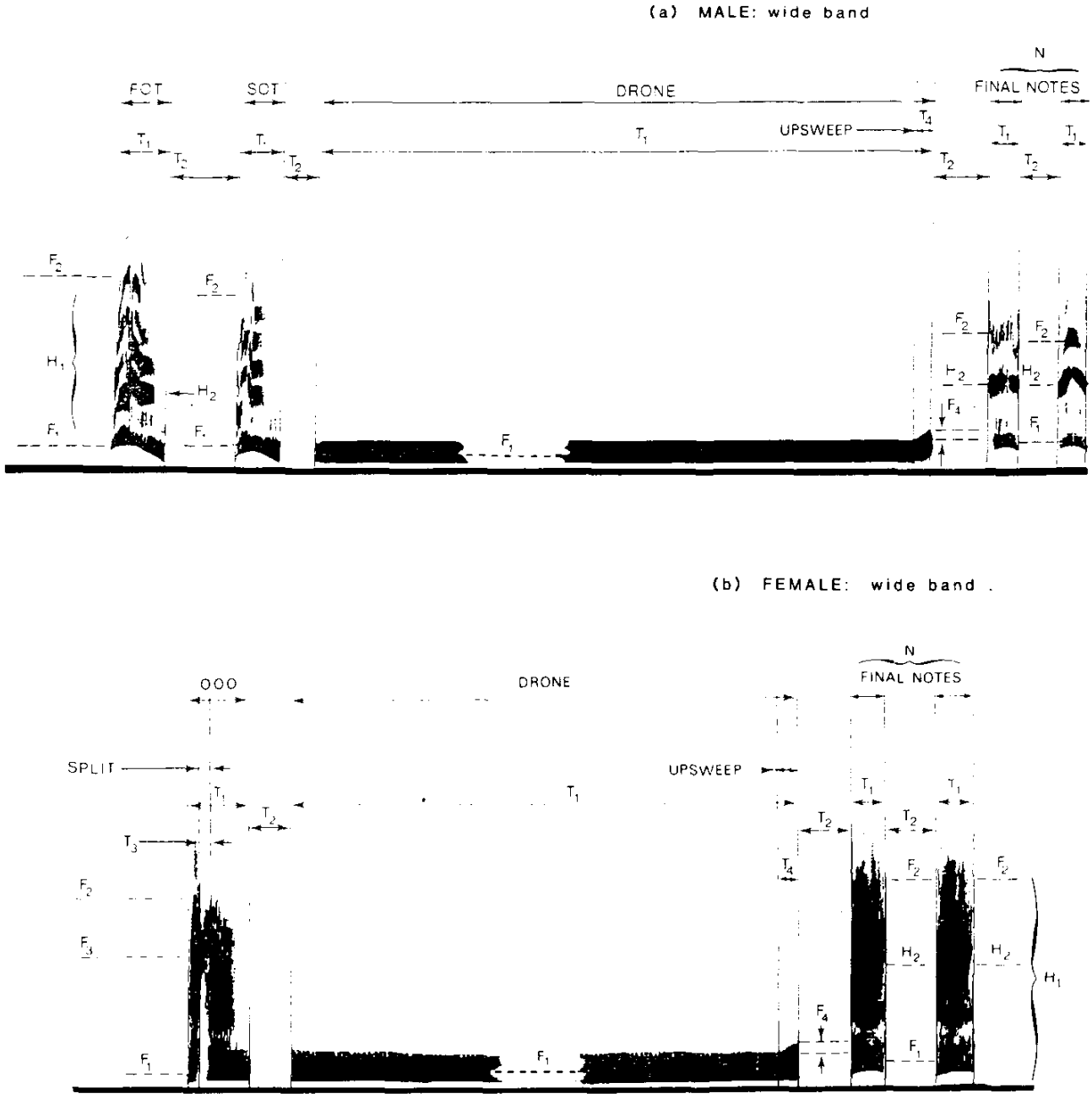

FIGURE 7 — Sonagrams of putative male and female calls showing the parameters measured

One or two syllables (FINAL) followed the DRONE in short calls, but this increased to 17 + in long calls. Most Coarse OOO, FOT and SOT syllables incorporated a SPLIT, which was a very small period when the frequency increased dramatically, leaving a gap in the low basic frequency, as in Fig. 7(b). No Sweet syllables incorporated a split. Wide-band sonagrams were used to measure 10 frequency (Hz or kHz), and narrow-band to measure time (ms). Usually, we could easily locate the harmonic containing the most energy by examining narrow-band sonagrams.

For the OOO, FOT and SOT syllables, the following measurements were made on both Sweet and Coarse calls: F1, the mean basic frequency (Hz) of the syllable; F2, the mean frequency (kHz) of the highest harmonic; T1,

the duration of the syllable; and T2, the interval between this and the next syllable. Harmonics were easily distinguished in the Sweet calls, whereas they were indistinguishable for all but three of the Coarse calls. H1, the number of harmonics, and H2, the harmonic that contained the maximum energy, were measured in the Sweet calls (and rarely, in Coarse calls). In the Coarse calls, F3, the frequency (kHz) of the maximum of the split, and T3, the duration of the split, were measured.

For the DRONE, five parameters were recorded. These were F1, the mean frequency (Hz) of the syllable; T1, the duration of the syllable; T2, the interval between the DRONE and the first of the FINAL syllables; F4, the increase in frequency (Hz) of the upsweep; and T4, the duration of the upsweep.

Six parameters were measured for the group of FINAL syllables. These were F1, the mean basic frequency (Hz); T1, the mean duration of the syllables; T2, the mean interval between the FINAL syllables; H1, the mean number of harmonics in the FINAL syllables; H2, the number of the harmonic showing the maximum energy; and N, the number of FINAL syllables.

Altogether, 35 parameters were measured, although at most 23 parameters were relevant to any one Sweet or Coarse call.

The Sweet and Coarse calls were compared, for each parameter common to both and without regard to island of origin, by means of frequency tabulations and t-tests. The data were then separated into two groups, comprising 155 Sweet and 165 Coarse calls. All subsequent analyses of vocalisation data were made separately on these two groups.

Using t-tests, we compared the mean of each parameter in the OOO syllable with the corresponding parameter in the FOT and SOT syllables, for each island sample and for the overall sample. One purpose of these tests was to determine which parameters (if any) of the OOO syllable matched corresponding parameters in the FOT and SOT syllables. The intention here was to maximise the sample sizes for further multivariate analysis, by pooling calls beginning with the OOO with calls beginning with the FOT. Because the FOT and SOT syllables are components of the same call, we applied paired t-tests to compare corresponding parameters of these syllables.

We applied one-way ANOVA to each of 23 parameters measured in the Sweet calls, and to each of the 23 parameters relevant to the Coarse calls, to test for differences among the four island samples. We include calls beginning withh the OOO syllable in these analyses, by identifying the OOO parameters with the equivalent SOT parameters.

The many significant results obtained in the ANOVAs for both Sweet and Coarse groups suggested that trial discriminant analyses might separate the four island subpopulations. As many cases were deficient in some parameter measurements, multivariate analysis using all variables as predictors was impractical. For each group, we had to choose a subset of the parameters that would give good discriminantion and at the same time provide enough cases for satisfactory analysis. For the Sweet calls we chose as predictors nine

parameters that had all been recorded in 90 of the 155 calls. These were F1(OOO/SOT), T1(OOO/SOT), T2(OOO/SOT), F1(DRONE), T1(DRONE), T2(DRONE), F1(FINAL), T2(FINAL) and H1(FINAL). For the Coarse calls, we used five parameters in the discriminant analysis: F2(OOO/SOT), T1(DRONE), T4(DRONE), F1(FINAL) and H2(FINAL). These had all been recorded in only 37 of the 165 Coarse calls.

For comparison purposes, we referred to recordings and prepared sonagrams of calls of other members of the *P. hasitata* superspecies held in the Library of Natural Sounds (LNS) at Cornell University.

RESULTS

Breeding phenology

The time of year at which Dark-rumped Petrels bred in Galapagos varied greatly among islands and within islands (Fig. 4). Laying dates on Santa Cruz averaged 4 July (SE 2.0 days) in 1978 and 5 July (SE 2.4 days) in 1979, and were highly clumped. Laying on Santiago was less synchronised, and the average laying date in 1979 was 7 May (SE 4.0).

On Floreana, eggs were laid continually from January to June. However, laying dates were associated with a geographical separation of the breeding colonies. We estimated dates for 22 eggs in a colony on Cerro Pajas (HAB), and for another 21 eggs on Cerro Alerie and Cerro Verde (LAB), which are both lower than Cerro Pajas. The average laying date for Floreana HAB in 1979 was 18 March (SE 4.1 days). For Floreana LAB it was 8 May (SE 4.8 days), significantly later ($t = 8.14$, 41 d.f., $P < 0.001$). Cerro Alerie is only 400 m from Cerro Pajas. F. and J. Cruz (pers. comm.) noted a similar range of laying dates in 1982 and 1983, and that laying on Cerro Verde and Cerro Alerie was about 1 month later than on Cerro Pajas.

On San Cristobal estimated laying dates extended from November to August; however, the pattern appeared to be bimodal (Fig. 4). We estimated that eggs were laid from 1 November to 10 March, and from 7 April to 20 June; two eggs (estimated 12 August) were presumed to belong in the second group. Thus there appeared to be two peaks: the average laying date of the first group was 9 January, and of the second group, 1 June 1979. In the statistical test for bimodality, the minimum variance sum statistic computed for the observed data was less than those similarly computed for 99.2% of 10 000 randomly generated uniform distributions. The separation date for which the minimum variance sum occurred for the observed data corresponded to the period 10 March to 7 April. One group of birds breeds at the end of the year (EOY), and the other in the middle of the year (MOY).

Differences among the mean sample dates were highly significant ($P < 0.001$). For the six populations identified here, all mean sample dates differed from each other (*a posteriori* contrast tests, Least Significant Difference, $P < 0.01$), except those for Santiago and Floreana LAB.

Morphology and weight

Very highly significant ($P < 0.001$) differences among the six Galapagos population samples were indicated by the one-way ANOVAs for the mensural variables bill depth, tarsus length, toe length, wing length and tail length;

TABLE 1 — One-way ANOVAs of morphology and plumage measurements indicate significant differences among population samples within Galapagos. The mean, standard deviation and number of birds in each sample are shown. All lengths are in mm, and weight in g.

		Santa Cruz	San Cristobal MOY	San Cristobal EOY	Santiago	Floreana LAB	Floreana HAB	*ANOVA*
Culmen Length	$\bar{X}$	33.2	33.0	33.3	33.7	34.3	34.1	$F_{5,120} = 3.38$
	SD	1.2	1.4	0.9	1.0	1.1	1.1	$P < 0.01$
	N	47	7	14	20	17	21	
Bill Depth	$\bar{X}$	11.2	10.6	11.0	11.1	11.5	11.7	$F_{5,120} = 6.65$
	SD	0.6	0.6	0.4	0.5	0.7	0.5	$P < 0.001$
	N	47	7	14	20	17	21	
Tarsus Length	$\bar{X}$	39.2	39.2	40.3	39.9	40.8	40.9	$F_{5,119} = 7.83$
	SD	1.3	1.3	0.9	0.8	1.6	1.3	$P < 0.001$
	N	45	7	15	20	17	21	
Toe Length	$\bar{X}$	39.2	38.8	40.4	40.0	41.7	40.8	$F_{5,119} = 7.41$
	SD	2.0	1.5	1.5	1.4	1.4	1.3	$P < 0.001$
	N	45	7	15	20	17	21	
Wing Length	$\bar{X}$	307	310	312	312	316	318	$F_{5,115} = 6.71$
	SD	7	13	5	7	8	8	$P < 0.001$
	N	42	7	15	20	16	21	
Tail Length	$\bar{X}$	141	145	145	145	146	146	$F_{5,112} = 5.79$
	SD	5	3	4	4	3	5	$P < 0.001$
	N	41	5	15	20	16	21	
Volume Index (x 0.001)	$\bar{X}$	160	151	164	164	176	176	$F_{5,110} = 15.0$
	SD	10	3	8	8	14	10	$P < 0.001$
	N	40	5	14	20	16	21	
Weight	$\bar{X}$	389	387	390	385	413	429	$F_{5,109} = 3.77$
	SD	40	38	38	30	40	43	$P < 0.01$
	N	37	7	14	20	17	20	
Forehead	$\bar{X}$	6.2	7.0	5.6	7.0	5.4	7.1	$F_{5,105} = 1.18$
	SD	3.0	3.5	2.5	2.8	2.4	1.8	Not Signif.
	N	35	7	14	20	16	19	
Collar	$\bar{X}$	5.6	4.8	–	6.2	6.7	5.3	$F_{4,78} = 1.09$
	SD	2.8	2.9	–	2.0	1.6	2.4	Not Signif.
	N	27	6	0	18	14	18	

and highly significant ($P<0.01$) differences for culmen length and weight (Table 1). These differences were considerably larger than the differences between the sexes for comparable characters measured by Gifford (*in* Loomis 1918) for the Molokai population in Hawaii, where males appeared to be slightly larger than females. Birds in Galapagos were first measured throughout the breeding season, and there is no reason to suspect that birds of one sex were encountered more frequently than the other: thus we do not expect any sex-related bias in morphology and weight measurements.

TABLE 2 — Summary of comparisons of six mensural variables among population samples, using *a posteriori* contrast tests following one-way ANOVAs. Values indicate the number of times that the mean for one population sample (shown at left) was significantly less than the corresponding mean for another sample (shown at top)

	San Cristobal		Santiago	Floreana	
	MOY	EOY		LAB	HAB
Santa Cruz	(1)*	3	3	6	6
San Cristobal MOY		1	0	4	5
San Cristobal EOY			0	3	3
Santiago				3	3
Floreana LAB					0

* The mean bill depth for Santa Cruz was significantly larger than the mean bill depth for San Cristobal MOY

A posteriori contrast tests between the sample means for each mensural variable strongly suggested that an ordering could be made based on size. For each of the six variables, we made 15 pair-wise comparisons among the six samples. From these 90 *a posteriori* contrast tests at the 0.05 probability level, four or five apparently significant differences between means would normally be expected to occur by chance. In our tests, 41 significant differences existed. Table 2 shows the number of times that a sample mean for one population was significantly less than the corresponding sample mean for another population. No significant differences were indicated between the two Floreana samples, and only one significant difference was found among San Cristobal MOY, San Cristobal EOY and Santiago. However, the means of all six variables for the Santa Cruz sample were significantly smaller than those for both Floreana samples, and were often significantly less than those for San Cristobal EOY and Santiago. Similarly, the means of both San Cristobal samples and the Santiago sample were often significantly less than those for the Floreana samples. *A posteriori* contrast tests indicated that the San Cristobal MOY sample means for toe and volume were significantly less than those for San Cristobal EOY.

As no morphological differences were found between the Floreana LAB and HAB samples, we pooled these before discriminant analysis. Following the results of the ANOVAs, we used a sample of 116 cases having no missing

TABLE 3 — Summary of discriminant analysis using five mensural variables to separate five populations within Galapagos

Standardised Coefficients			Population Centroids		
Function	1	2	Function	1	2
Bill Depth	0.028	1.002	Santa Cruz	-0.959	0.384
Tarsus Length	0.518	0.256	San Cristobal MOY	-0.874	-1.563
Toe Length	0.403	0.106	San Cristobal EOY	0.268	-0.700
Wing Length	0.254	-0.105	Santiago	0.056	-0.427
Tail Length	0.423	-0.378	Floreana	1.023	0.291
Eigenvalue	0.724	0.286			
% of Variance	67.9	26.8			

values for the variables bill depth, tarsus, toe, wing length and tail length. Two discriminant functions explained 94.7% of the total between-samples variability (Table 3), and these were used in a subsequent classification of cases. The overall Wilks' lambda for the analysis was 0.427, with a corresponding chi-squared statistic of 93.7 (20 DF, $P<0.001$).

The sample centroids given by the first discriminant function tend to separate the samples into three groups: Santa Cruz and San Cristobal MOY, with low values; San Cristobal EOY and Santiago, moderate values; and Floreana, high values. These coarse groupings can be directly perceived in the sample means for tarsus and toe, and to a lesser extent for wing length and tail length. Thus the first function relates to the size of the birds. Inspection of the discriminant function coefficients and the pooled within-samples correlation coefficients indicates that it is these four variables that load most strongly on the first discriminant function.

Good separation between the Santa Cruz and San Cristobal MOY samples is given by the second discriminant function, which is related to differences in shape. The dominant contribution to this function is from bill depth, for which the San Cristobal MOY sample has the lowest mean, and for which the Santa Cruz sample has the second highest mean, after Floreana. Further separation of the Santa Cruz sample from the other four is gained by the negatively loaded variable tail length. The mean tail length for Santa Cruz is less than that for all other samples.

A sudsequent classification of the 116 birds into sample groups, based on the two discriminant functions, achieved a classification rate of 58% (Table 4). This compares well with the *a priori* probability of correct classification of 20%. The 15 incorrectly classified birds from Santiago sample were distributed uniformly across the other samples: Santa Cruz (3), San Cristobal MOY (3), San Cristobal EOY (5), and Floreana (4).

TABLE 4 — Results of classification of birds into source populations following discriminant analysis

	Sample Size	Correctly Classified	Percentage Correct
Santa Cruz	40	24	60.0
San Cristobal MOY	5	4	80.0
San Cristobal EOY	14	8	57.1
Santiago	20	5	20.0
Floreana	37	27	73.0
Total	116	68	58.6

TABLE 5 — Student's t-tests of morphology measurements indicate significant differences between Galapagos and Hawaiian population samples. The mean, standard deviation and number of birds in each sample are shown. All lengths are mm

	Galapagos			Hawaii			Student's t-test		
	$\bar{X}$	SD	N	$\bar{X}$	SD	N	t	df	P
Culmen Length	33.6	1.2	127	31.1	1.5	8	5.58	133	<0.001
Bill Depth	11.3	0.6	127	10.6	0.7	10	3.29	135	<0.01
Tarsus Length	40.0	1.4	128	37.8	1.5	11	4.73	137	<0.001
Toe Length	40.0	1.8	129	39.5	1.7	11	0.97	138	N.S.
Wing Length	312	9	125	291	8	11	7.54	134	<0.001
Tail Length	144	5	119	139	7	8	2.56	125	<0.05
Volume Index	165	13	117	143	15	8	4.76	123	<0.001

The results of comparing the Hawaiian and combined Galapagos samples are shown in Table 5. For each measurement, the mean for Hawaii was less than that for Galapagos. The differences were very highly significant ($P<0.001$) for culmen length, tarsus, wing length and notional volume; highly significant ($P<0.01$) for bill depth; significant ($P<0.05$) for tail length; and not significant for toe. For all measurements except toe, the Hawaii mean was less than the smallest of the Galapagos means.

Eggs

Significant differences ($P<0.05$) existed among the mean breadths and volumes of eggs taken from the four islands (Table 6). No significant difference was found among mean lengths. *A posteriori* contrast tests indicated that eggs from San Cristobal were significantly smaller than those from Santiago and Floreana; eggs from Santa Cruz were significantly smaller those from Floreana. Thus differences in egg size corresponded approximately with the patterns apparent in bird size. Comparisons of the

lengths and breadths of eggs from Hawaii (Simons 1985) and Galapagos showed significant differences ($P<0.001$, Table 7). Hawaiian eggs were on average 5% longer and 6% broader than Galapagos eggs, implying an 18% larger volume.

TABLE 6 — Results of one-way ANOVAs comparing egg dimensions (mm) among Galapagos populations. The mean, standard deviation and number of eggs are shown for each sample

		Santa Cruz	San Cristobal	Santiago	Floreana	*ANOVA*
Length	$\bar{X}$	60.84	60.87	61.10	62.03	$F_{3,55}= 0.26$
	SD	2.18	1.63	1.55	2.14	
	N	18	9	13	19	Not Signif.
Breadth	$\bar{X}$	43.79	42.79	44.02	44.34	$F_{3,55}= 3.52$
	SD	1.37	1.10	0.99	1.18	
	N	18	9	13	19	$P < 0.05$
Volume	$\bar{X}$	116.8	111.5	118.5	122.1	$F_{3,55}= 3.85$
Index	SD	8.3	6.3	5.8	9.3	
(x 0.001)	N	18	9	13	19	$P < 0.05$

TABLE 7 — Student's t-tests comparing the dimensions (mm) of Galapagos and Hawaiian eggs. The mean, standard deviation and number of eggs are shown for each sample

	Galapagos			Hawaii			Student's t-test		
	$\bar{X}$	SD	N	$\bar{X}$	SD	N	t	df	P
Length	61.28	1.99	59	64.45	2.88	30	5.56	87	<0.001
Breadth	43.87	1.27	59	46.47	1.37	30	8.69	87	<0.001

Plumage

ANOVA indicated no significant plumage differences among population samples (Table 1); nor was the Pearson correlation coefficient between forehead and collar significant ($r = 0.1466$ for 83 birds).

There seems to be very little variation in the almost white forehead (i.e. score of 1 in Fig. 5) in Dark-rumped Petrels from Hawaii (Henshaw 1902; Baldwin & Hubbard 1949, Fig. 43; Richardson & Woodside 1954, Fig. 3; Pratt *et al.* 1987; Berger 1983). Researchers at the Bishop Museum in Honolulu reached the same conclusion (Anon 1908). Little information about collar patterns in Hawaiian birds is available.

TABLE 8 — Results of t-tests comparing parameters common to Sweet (putative male) and Coarse (putative female) calls. The mean, standard deviation and number of calls are shown for each sample

		Sweet Calls			Coarse Calls			Student's t-test		
		$\bar{X}$	SD	N	$\bar{X}$	SD	N	t	df	P
OOO	F1	705	67	54	334	77	39	24.75	91	<0.001
	F2	4.70	0.63	45	3.99	0.97	44	4.10	87	<0.001
	F3	–	–	0	3.08	0.65	28			
	T1	106	31	54	118	32	47	–1.79	99	N.S.
	T2	88	71	54	75	49	47	1.08	99	N.S.
	T3	–	–	0	18	11	32			
	H1	4.51	0.79	49	–	–	0			
	H2	1.29	0.73	14	–	–	0			
FOT	F1	797	98	85	331	62	80	36.19	163	<0.001
	F2	4.75	0.84	84	4.37	0.74	85	3.15	167	<0.01
	F3	–	–	0	3.35	0.66	65			
	T1	91	21	85	94	25	85	–0.94	168	N.S.
	T2	140	29	90	121	30	88	4.30	176	<0.001
	T3	–	–	0	23	16	64			
	H1	4.2	1.2	85	12.0	4.2	2			
	H2	1.7	0.9	27	7.0	5.7	2			
SOT	F1	706	84	88	333	70	77	30.77	163	<0.001
	F2	4.45	0.83	80	4.01	0.80	85	3.40	163	<0.001
	F3	–	–	0	3.15	0.63	51			
	T1	105	19	88	112	30	86	–1.97	172	N.S.
	T2	90	67	88	53	40	86	4.42	172	<0.001
	T3	–	–	0	13	5	60			
	H1	4.46	1.09	80	9.00	–	1			
	H2	1.42	0.81	26	–	–	0			
DRONE	F1	515	47	146	497	43	135	3.34	279	<0.001
	F4	264	101	130	230	83	103	2.76	231	<0.01
	T1	99	30	141	86	25	127	3.83	266	<0.001
	T2	89	31	135	87	19	139	0.69	272	N.S.
	T4	38	14	130	35	11	103	1.55	231	N.S.
FINAL	F1	674	77	127	291	51	109	44.22	234	<0.001
	T1	61	8	131	63	8	118	–2.16	247	<0.05
	T2	104	17	106	104	18	93	–0.05	197	N.S.
	H1	4.6	0.9	124	14.0	2.3	87	–41.41	209	<0.001
	H2	2.2	1.3	20	5.3	2.3	69	–5.77	87	<0.001
	N	4.8	3.7	131	3.9	2.5	118	2.12	247	<0.05

Vocalisations

Table 8 shows summary statistics and the results of t-tests comparing the Sweet and Coarse calls, for each variable common to both. Complete or almost complete separation existed in the following parameters:

A split existed in Coarse OOO, FOT and SOT syllables. None was detected in these Sweet syllables.

Harmonics of the Sweet OOO, FOT and SOT syllables could usually be measured; only rarely could these be measured for the same Coarse syllables.

For Sweet calls, the average basic frequency of the OOO syllable F1(OOO) was measured at less than 615 Hz for only three calls. For Coarse calls it exceeded 585 Hz only once. For Sweet calls, the average basic frequency of the FOT syllable F1(FOT) was always at least 585 Hz, but for Coarse calls it never exceeded 550 Hz.

For Sweet calls, the average basic frequency of the SOT syllable F1(SOT) was less than 610 Hz for only 11 calls, whereas for Coarse calls it exceeded 500 Hz for only three calls.

For Sweet calls, the average basic frequency of the FINAL syllables F1(FINAL) was always at least 500 Hz, whereas for Coarse calls it did not exceed 450 Hz.

With two exceptions, the number of harmonics measured in the FINAL syllables H1(FINAL) varied between 2 and 7 for Sweet calls and between 9 and 20 for Coarse calls. One Sweet and one Coarse call each had 8 harmonics.

Of the 23 t-tests comparing parameters common to both Sweet and Coarse calls, 16 tests were significant (Table 8). The mean F1 of each of the Sweet OOO, FOT, SOT and FINAL syllables was more than twice the mean of the Coarse counterpart; these differences were highly significant ($P<0.001$). For 63% of the Sweet calls and 30% of the Coarse calls, F1(DRONE) was measured at 500 Hz. While the mean F1 for the Sweet DRONE (515) appeared to be comparable with that for the Coarse (497), the difference was nevertheless significant ($P<0.001$). Similarly, the means of F2 for the OOO, FOT and SOT syllables in the Sweet calls were significantly higher than those for the Coarse calls. The upsweep (F4, DRONE) was also more pronounced for Sweet calls. No significant differences existed for the mean duration, T1, of the OOO, FOT and SOT syllables. T1(DRONE) was significantly longer for Sweet calls ($P<0.001$), and T1(FINAL) was significantly longer ($P<0.05$) for Coarse calls.

Comparison of OOO, FOT and SOT syllables

The results of t-tests aimed at matching these introductory syllables were conclusive. For the Sweet calls, only 2 out of 29 comparisons made between the OOO and SOT syllables showed a significant difference. No significant differences were noted between mean values of parameters measured for the overall sample. By contrast, 10 out of 28 comparisons between the OOO and FOT syllables, and 14 out of 28 comparisons between the FOT and SOT syllables showed significant differences. For the Coarse calls, 5 out of 30 comparisons of OOO and SOT parameters showed a significant

difference; 10 of the 30 comparisons of the OOO and FOT parameters and 18 out of 30 comparisons of the FOT and SOT parameters showed significant differences.

On the basis of these results, for both the Sweet and Coarse calls, we concluded that the OOO and SOT syllables were statistically similar and that the OOO and SOT both differed from the FOT syllable. In subsequent analyses, we treated corresponding parameters of the OOO and SOT syllables as equivalent.

Interisland comparisons – Sweet calls

Significant differences were found for 14 parameters of the Sweet calls (Table 9). Parameters for which the populations showed the greatest differences were:

F1, the average frequency, for the OOO/SOT, DRONE and FINAL syllables;

T1, the average duration, for the OOO/SOT and DRONE syllables;

T2, the following interval, for the OOO/SOT, DRONE and FINAL syllables; and

H2, the harmonic with maximum energy in the OOO/SOT syllable.

For parameters which showed significant differences among the populations, *a posteriori* contrast tests were applied (Least Significant Difference, $P<0.05$). Each parameter tended to distinguish different subsets of the islands; no consistent pattern was apparent for the interisland differences. Thus, for F1(OOO/SOT), the means for San Cristobal and Santiago were 673 and 664, whereas for Santa Cruz and Floreana the means were 731 and 744 (Table 9). For F1(DRONE), the mean for Floreana was 573; the means for Santa Cruz, San Cristobal and Santiago were 497, 503 and 497 respectively. For T2(OOO/SOT), the mean for San Cristobal was 30; for Santa Cruz, Santiago and Floreana, the means were 110, 98 and 109 respectively. These results suggested that, taken together in a multivariate analysis, these parameters would provide formidable discriminating power.

The parameter H2(OOO/SOT) had been measured for only 40 calls and was discarded in the subsequent discriminant analysis. Four other parameters, F1(FOT), H1(FOT), H2(FOT) and F4(DRONE), for which significant or highly significant differences among populations were shown were also omitted from the discriminant analysis because including these parameters would have severely restricted the number of cases.

Pearson correlation coefficients calculated for pairs of the nine predictor variables were generally low. A principal components analysis of these variables generated four factors whose eigenvalues exceeded 1.0 and which among them accounted for 66% of the variance. However, the subsequent varimax rotation produced no useful or recognisable groupings of the parameters.

Three discriminant functions were generated by the analysis, giving excellent separation of the four island populations. Wilks' lambda for all three functions combined was 0.118 with a corresponding chi-squared value of 176.1 (27 d.f., $P<0.001$), and for the third (and least significant function) alone, Wilks' lambda was 0.646 with a corresponding chi-squared value of 36.1 (7 d.f., $P<0.001$).

TABLE 9 — One-way ANOVAs of parameters measured in Sweet calls indicate significant differences among population samples within Galapagos. The mean, standard deviation and number of measurements in each sample are shown

			Santa Cruz	San Cristobal	Santiago	Floreana	*ANOVA*
FOT	F1	Mean	824	803	735	816	$F_{3,81} = 4.31$
		SD N	81 30	90 10	105 21	97 24	$P < 0.01$
	F2	Mean	4.77	4.31	4.85	4.82	$F_{3,80} = 0.98$
		SD N	0.93 30	1.08 9	0.84 21	0.56 24	Not Signif.
	T1	Mean	87	99	97	88	$F_{3,81} = 1.57$
		SD N	19 30	26 10	17 21	22 24	Not Signif.
	T2	Mean	147	130	138	138	$F_{3,86} = 1.14$
		SD N	27 30	23 12	31 23	33 25	Not Signif.
	H1	Mean	3.9	3.8	4.8	4.4	$F_{3,81} = 3.25$
		SD N	1.0 30	1.1 10	1.4 21	1.1 24	$P < 0.05$
	H2	Mean	–	–	1.3	2.2	$F_{1,25} = 6.81$
		SD N	– 0	– 0	0.8 15	0.8 12	$P < 0.05$
OOO & SOT	F1	Mean	731	673	664	744	$F_{3,138} = 11.3$
		SD N	78 48	53 31	70 33	73 30	$P < 0.001$
	F2	Mean	4.67	4.23	4.58	4.51	$F_{3,121} = 1.59$
		SD N	0.97 44	0.51 20	0.74 32	0.54 29	Not Signif.
	T1	Mean	114	82	114	106	$F_{3,138} = 17.4$
		SD N	22 48	24 31	18 33	18 30	$P < 0.001$
	T2	Mean	110	30	98	109	$F_{3,138} = 12.7$
		SD N	54 48	47 31	70 33	75 30	$P < 0.001$
	H1	Mean	4.2	4.3	4.8	4.6	$F_{3,125} = 2.61$
		SD N	1.1 45	1.2 23	0.6 32	0.9 29	Not Signif.
	H2	Mean	1.0	1.0	1.2	3.0	$F_{3,36} = 23.9$
		SD N	0.0 2	0.0 12	0.6 21	0.0 5	$P < 0.001$
DRONE	F1	Mean	497	503	497	573	$F_{3,142} = 36.2$
		SD N	27 48	8 33	16 33	67 32	$P < 0.001$
	F4	Mean	261	300	263	222	$F_{3,126} = 2.75$
		SD N	88 45	120 31	87 32	101 22	$P < 0.05$
	T1	Mean	851	956	1154	1071	$F_{3,137} = 8.49$
		SD N	255 48	350 33	259 32	257 28	$P < 0.001$
	T2	Mean	78	109	93	79	$F_{3,131} = 8.69$
		SD N	15 43	25 31	49 30	17 31	$P < 0.001$
	T4	Mean	40	41	35	35	$F_{3,126} = 1.68$
		SD N	14 45	11 31	15 32	15 22	Not Signif.
FINAL	F1	Mean	630	728	650	707	$F_{3,123} = 16.3$
		SD N	69 43	48 28	61 26	80 30	$P < 0.001$
	T1	Mean	61	60	62	60	$F_{3,127} = 0.64$
		SD N	6 43	6 28	10 30	9 30	Not Signif.
	T2	Mean	101	116	97	107	$F_{3,102} = 6.54$
		SD N	19 34	18 23	10 29	15 20	$P < 0.001$
	H1	Mean	4.6	4.2	4.6	5.1	$F_{3,120} = 5.09$
		SD N	0.9 42	0.9 26	0.7 29	0.9 27	$P < 0.01$
	H2	Mean	1.0	2.3	2.9	1.9	$F_{3,16} = 1.49$
		SD N	0.0 2	0.6 3	1.5 7	1.2 8	Not Signif.
	N	Mean	4.2	4.9	6.3	4.0	$F_{3,127} = 2.54$
		SD N	3.2 43	3.5 28	4.1 30	3.9 30	Not Signif.

TABLE 10 — Summary of two discriminant analyses, one of Sweet calls and one of Coarse calls, which distinguish four island populations within Galapagos. Standardised discriminant function coefficents are shown for the 3 functions derived in each analysis

	Sweet Calls			Coarse Calls		
Function	1	2	3	1	2	3
F1 (OOO/SOT)	-0.27	0.27	-0.64			
F2 (OOO/SOT)				-0.05	-0.04	0.86
T1 (OOO/SOT)	-0.56	0.11	0.38			
T2 (OOO/SOT)	0.12	0.39	0.34			
F1 (DRONE)	0.40	0.72	0.12			
T1 (DRONE)	0.43	-0.03	0.67	-0.07	0.61	0.16
T2 (DRONE)	0.26	-0.32	0.42			
T4 (DRONE)				0.49	-0.01	-0.47
F1 (FINAL)	0.73	0.08	0.04	0.86	0.20	0.43
T2 (FINAL)	0.46	0.16	-0.35			
H1 (FINAL)	0.10	0.37	0.14			
H2 (FINAL)				0.05	0.80	-0.21
Eigenvalue	1.57	1.12	0.55	1.13	0.70	0.30
% of Variance	48.5	34.6	16.9	53.2	32.8	14.1
Population Centroids:						
Santa Cruz	-1.29	0.16	-0.60	0.33	-0.50	-0.46
San Cristobal	1.52	-1.22	-0.43	1.51	-0.34	1.03
Santiago	-0.50	-0.44	1.20	-1.43	0.02	0.30
Floreana	1.36	2.01	0.12	0.58	1.92	-0.21

Discriminant functions were evaluated at each of the population centroids (Table 10). The first function distinguishes the Santa Cruz and Santiago populations from the San Cristobal and Floreana populations. The second function separates the Floreana population from the other three (and in particular, from the San Cristobal population). The third function tends to isolate the Santiago population.

As with the prior factor analysis, no meaningful pattern or relationship appears to exist among variables that load strongly on any one function (indicated by the standardised discriminant function coefficients, Table 10). Several variables load strongly on two functions. Relationships between the variables and discriminant functions may be further understood by reference to the prior one-way ANOVAs. For example, the ANOVA for F1(DRONE) indicated a mean of 573 for the Floreana population, whereas the means for the other three populations were near 500. Thus, F1(DRONE) loads most heavily on the second discriminant function, which tends to distinguish Floreana.

Analysis of the 90 calls used to compute the discriminant functions correctly classified 74 (82.2%) of these calls (Table 11). A further 38 calls, not used in the analysis and for which up to three of the classification parameters had not been measured, were also subsequently classified, with values for the missing parameters replaced by the overall sample means. Despite these missing values, 27 (71.1%) of the 38 calls were correctly classified, giving an overall classification rate of 101 in 128 cases (78.9%). These classification rates compare very favorably with the *a priori* probability (25%) that a randomly chosen call will be correctly classified. Separation of the populations is clearly indicated in the scatter diagrams (Fig. 8) for these 128 calls.

TABLE 11 — Results of classification of birds into island populations following discriminant analysis using vocalisation parameters of Sweet calls. Values in parentheses show the classification results when 38 additional cases with up to three missing measurements are included

	Sample Size	Correctly Classified	Percentage Correct
Santa Cruz	32 (42)	27 (34)	84.4 (81.0)
San Cristobal	21 (29)	18 (26)	85.7 (89.7)
Santiago	22 (30)	18 (23)	81.8 (76.7)
Floreana	15 (27)	11 (18)	73.3 (66.7)
Total	90 (128)	74 (101)	82.2 (78.9)

Interisland comparisons – Coarse calls

For the Coarse calls, the number of significant differences among islands indicated by the one-way ANOVAs contrasted strongly with the results for the Sweet calls. Significant differences were indicated among the populations for only seven parameters, F1(DRONE), F1(FINAL), F2(OOO/SOT), T1(DRONE), T4(DRONE), H2(FINAL) and N(FINAL) (Table 12); and no significant differences for 16 parameters.

The incomplete nature of the data severely restricted multivariate analysis of the Coarse calls. For example, in 165 calls, 129 measurements were made of F2(OOO/SOT), 127 of T1(DRONE), 103 of T4(DRONE), 109 of F1(FINAL) and 69 of H2(FINAL). However, the full set of these five parameters was measured in only 37 calls. Thus, the results of the analysis which we report here, while encouraging, must be regarded as speculative.

As would be expected from the fewer significant results obtained in the one-way ANOVA of Coarse calls, discrimination between the four island populations was not as successful as for the Sweet calls. As with the Sweet calls, three discriminant functions were generated (Table 10), with an overall Wilks' lambda (all three functions combined) of 0.213, with corresponding chi-squared = 48.8 (15 d.f., $P<0.001$). Wilks' lambda for the third function alone was 0.770, and this is also significant ($P<0.05$).

No obvious relationships among the predictor variables are apparent from the way in which these load on the discriminant functions. The discriminating power of F1(FINAL) is clear in both the one-way ANOVA

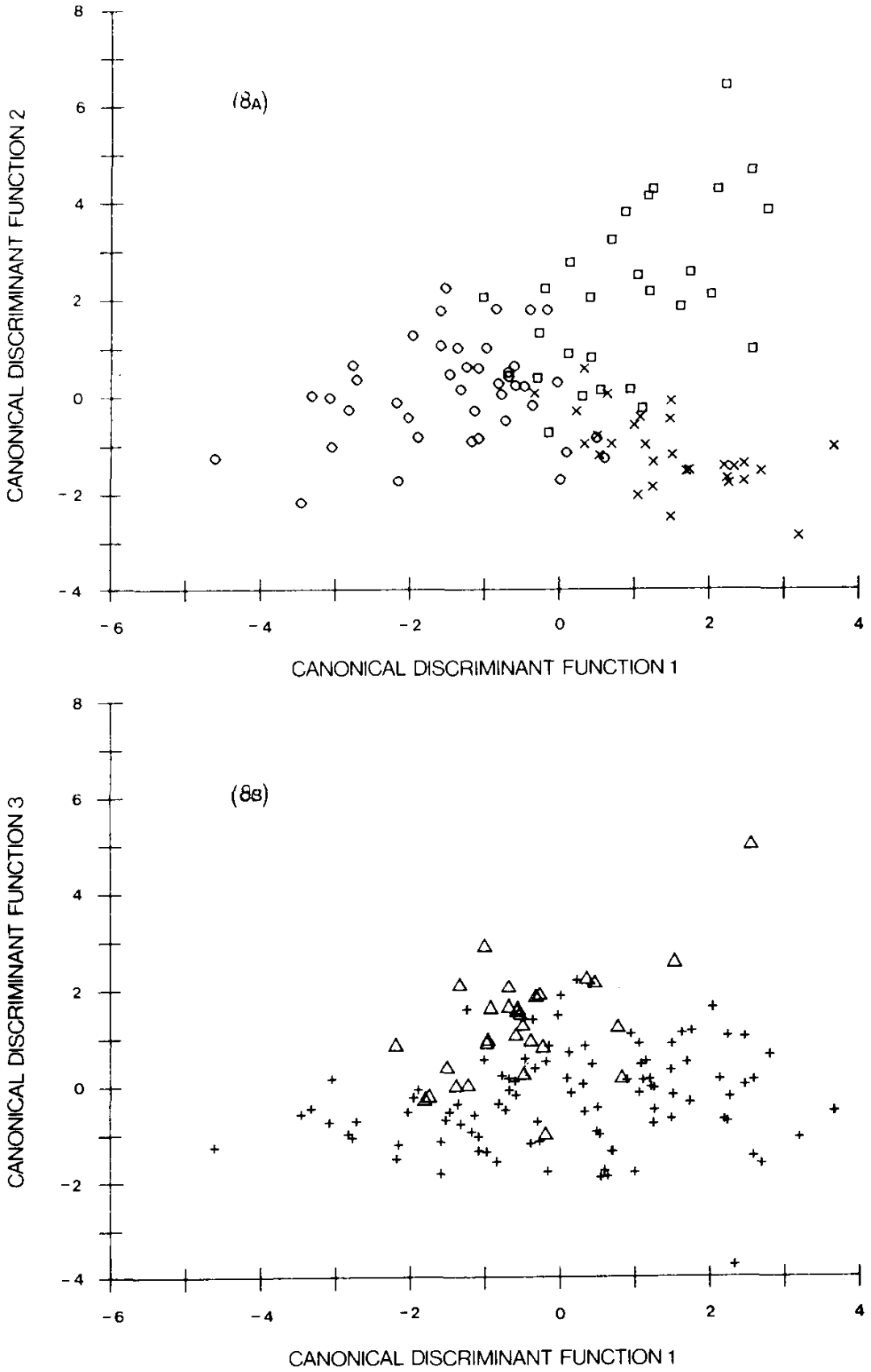

FIGURE 8 —Scatter diagrams showing the classification for 128 putative male Dark-rumped Petrel calls following discriminant analysis. The first two discriminant functions (8A) separate the Santa Cruz (O), San Cristobal (X) and Floreana (□) populations. The third discriminant function (8B) separates Santiago (△) from the other three populations (+)

TABLE 12 —One-way ANOVAs of parameters measured in Coarse calls indicate significant differences among population samples within Galapagos. The mean, standard deviation and number of measurements in each sample are shown.

			Santa Cruz	San Cristobal	Santiago	Floreana	*ANOVA*
FOT	F1	Mean	339	342	314	348	$F_{3,76} = 1.28$
		SD N	80 27	29 12	51 30	62 11	Not Signif.
	F2	Mean	4.12	4.40	4.60	4.30	$F_{3,81} = 2.32$
		SD N	0.92 28	0.62 14	0.50 32	0.82 11	Not Signif.
	F3	Mean	3.21	3.85	3.25	3.36	$F_{3,61} = 2.60$
		SD N	0.73 24	0.54 10	0.51 23	0.81 8	Not Signif.
	T1	Mean	91	87	96	110	$F_{3,81} = 2.17$
		SD N	22 28	21 14	27 32	26 11	Not Signif.
	T2	Mean	123	111	119	133	$F_{3,84} = 1.22$
		SD N	28 29	30 16	34 32	17 11	Not Signif.
	T3	Mean	19	21	24	31	$F_{3,60} = 1.45$
		SD N	16 24	12 10	14 22	20 8	Not Signif.
OOO & SOT	F1	Mean	347	325	324	325	$F_{3,112} = 0.88$
		SD N	88 44	41 20	75 38	33 14	Not Signif.
	F2	Mean	3.70	4.17	4.29	3.98	$F_{3,125} = 4.25$
		SD N	1.14 50	0.41 23	0.53 42	0.72 14	$P < 0.01$
	F3	Mean	2.95	3.28	3.27	3.05	$F_{3,75} = 1.68$
		SD N	0.75 32	0.53 14	0.54 27	0.43 6	Not Signif.
	T1	Mean	119	111	111	111	$F_{3,129} = 0.64$
		SD N	29 54	24 23	38 42	24 14	Not Signif.
	T2	Mean	60	47	64	80	$F_{3,129} = 1.80$
		SD N	42 54	41 23	47 42	46 14	Not Signif.
	T3	Mean	13	15	16	19	$F_{3,88} = 1.36$
		SD N	6 39	11 17	7 29	12 7	Not Signif.
DRONE	F1	Mean	493	508	487	521	$F_{3,131} = 3.36$
		SD N	45 54	29 24	42 41	41 16	$P < 0.05$
	F4	Mean	224	255	232	194	$F_{3,99} = 1.25$
		SD N	87 47	77 21	86 26	58 9	Not Signif.
	T1	Mean	788	793	894	1135	$F_{3,123} = 8.69$
		SD N	208 53	136 22	277 39	298 13	$P < 0.001$
	T2	Mean	91	80	85	87	$F_{3,135} = 1.86$
		SD N	22 49	15 22	18 54	17 14	Not Signif.
	T4	Mean	35	35	32	48	$F_{3,99} = 5.04$
		SD N	10 47	11 21	11 26	12 9	$P < 0.01$
FINAL	F1	Mean	291	340	261	292	$F_{3,105} = 13.6$
		SD N	45 43	42 20	44 34	42 12	$P < 0.001$
	T1	Mean	64	64	60	65	$F_{3,114} = 2.06$
		SD N	7 49	6 20	10 36	8 13	Not Signif.
	T2	Mean	108	98	104	103	$F_{3,89} = 1.22$
		SD N	21 38	14 17	19 27	12 11	Not Signif.
	H1	Mean	13.4	13.5	14.5	14.9	$F_{3,83} = 2.13$
		SD N	2.2 33	1.6 12	2.6 32	1.5 10	Not Signif.
	H2	Mean	4.5	4.3	5.3	8.8	$F_{3,65} = 9.76$
		SD N	1.7 22	2.4 7	1.9 32	2.5 8	$P < 0.001$
	N	Mean	3.7	5.0	3.3	4.8	$F_{3,114} = 2.73$
		SD N	2.4 49	2.5 20	2.4 36	2.9 13	$P < 0.05$

and its high correlation with the first discriminant function. This function separates the Santiago population from the pair Santa Cruz and Floreana, which in turn are separated from the San Cristobal population. The second discriminant function, on which T1(DRONE) and H2(FINAL) load heavily, tends to isolate the Floreana population.

Despite the few cases used in the analysis, separation of the four populations was generally good. Twenty-seven (73.0%) of the 37 calls used to compute the discriminant analysis were subsequently correctly classified (Table 13). For another 74 cases with one or two missing measurements which were also classified (again replacing missing values by the total sample means), 42 (56.8%) were correctly classified. Overall, 69 cases (62.2%) were classified correctly out of 111.

TABLE 13 — Results of classification of birds into island populations following discriminant analysis using vocalisation parameters of Coarse calls. Values in parentheses show the classification results when 74 additional cases with one or two missing measurements are included

	Sample Size	Correctly Classified	Percentage Correct
Santa Cruz	16 (46)	11 (29)	68.8 (63.0)
San Cristobal	5 (22)	4 (15)	80.0 (68.2)
Santiago	11 (31)	8 (17)	72.7 (54.8)
Floreana	5 (12)	4 (8)	80.0 (66.7)
Total	37 (111)	27 (69)	73.0 (62.2)

DISCUSSION

Breeding phenology

Eggs were laid in most months of the year somewhere in the Galapagos archipelago. However, the situation is unusual in that the same species breeds not only at different times of the year on different islands, but also at different times of the year on the same islands. The spread of laying dates also varies considerably among populations.

On Santa Cruz the average laying dates in two consecutive years differed by one day. However, the breeding timetable on Santa Cruz could have been different, or at least more protracted, as recently as 20 or 30 years ago, when the population numbered hundreds of thousands and birds bred in a greater variety of burrow locations. On 18 December 1952, Robert I. Bowman (pers. comm.) heard calling birds flying inland. Local inhabitants claimed that the birds were returning to start breeding. He also found a young bird near fledging in a burrow on Santa Cruz on 3 March 1962 (pers. comm.), two or three months after fledglings have departed in recent years.

Differences between the breeding phenologies of the LAB and HAB colonies on Floreana may be related to differences in air temperature and humidity: when the top of the high colony was in cloud, the low colonies were often cloud-free, although altitudes differ by only 120 m.

Loomis (1918) stated that the species was found throughout the year in Galapagos waters, and Castro (*in* Harris 1970) thought that the species may remain near San Cristobal in small numbers from January to April. These observations suggest that birds on San Cristobal may breed all year. This current study shows that, rather than laying randomly throughout the year, they breed in two distinct groups, MOY and EOY. It is difficult to formulate alternative null hypotheses against which the hypothesis of bimodality can be tested; however, the result of the statistical test for bimodality on San Cristobal is persuasive ($P<0.01$). Whether MOY and EOY birds breed consistently in the same group over a period of years has not been investigated, but it is likely that they do; possible size differences between the two groups are documented in this study. The most obvious difference between the two groups is that MOY eggs are laid in cold and wet ambient conditions, whereas EOY eggs are laid in hot and humid conditions. Temperature and humidity (as well as other factors) influence embryo development (Drent 1975). Thus, unless the construction of burrows on San Cristobal (and Floreana) produces a microclimate that minimises variations within the nest chamber, evolutionary compensations are likely to have been made to accommodate temperature and humidity differences. These compensations might be changes in egg size, shell thickness and porosity, incubation period and intensity of incubation. None of these was examined in this study.

Because of the large area of apparently suitable breeding habitat on Floreana and San Cristobal before major habitat alteration began 30 years ago, it is unlikely that a scarcity of nest sites contributed to these differences in the timing of the breeding cycles of Dark-rumped Petrels there. Many reasons have been proposed for the great variation of the breeding cycles of tropical seabirds. Harris (1984) summarised the variable breeding cycles of Galapagos seabirds, and suggested (Harris 1969) that food availability was not likely to be a major factor causing summer and winter populations of Band-rumped Storm Petrels (*Oceanodroma castro*) to breed on Isla Plaza, Galapagos. However, so little is known about factors such as diet, feeding locations and physiology which may affect Dark-rumped Petrel breeding phenology, that further discussion of these fascinating interpopulation differences is pointless at this stage.

Morphology

The morphology analyses highlighted interpopulation differences in the size and shape of birds in Galapagos. Populations that are similar in size breed at different times of the year, e.g. those of San Cristobal EOY and Santiago, or the two Floreana populations. The populations of Floreana LAB, San Cristobal MOY and Santiago differ significantly in size and breed at similar times of the year.

Birds on Santa Cruz had disproportionately deep bills and short tails; no other differences in shape among the populations were apparent. It is interesting to speculate why bill depth on Santa Cruz is relatively large. As recently as the 1930s, Dark-rumped Petrel numbers on Santa Cruz were very high, and many nested in very shallow burrows, under matted roots, and on the surface (Harris 1970, Tomkins 1985). If small-billed birds tended to breed near the surface and were thus more easily killed by predators, the remaining population would probably be deep burrowers, i.e. birds with strong, deep bills.

The oceanic and climatic conditions to the north and south of the archipelago vary considerably from the (southern) summer to winter. Although it is not known where these birds feed during their breeding season, observations by RJT suggest that birds from Santiago fly north, those from Floreana fly south, and from Santa Cruz, southeast. Populations with different flight abilities may feed on different prey size or in different climatic or oceanic regimes. For example, as tail length is one determinant of flight performance, it is possible that the shorter tails of the Santa Cruz birds allow them to manoeuvre differently whilst chasing prey. Large numbers of Dark-rumped Petrels have been seen feeding in the eastern tropical Pacific Ocean (Loomis 1918, Murphy 1936, Pitman 1982), but their origins and breeding status are unknown.

Plumage

With a few outstanding exceptions, the overall dark dorsal and white ventral plumage colours are similar in most species of *Pterodroma*, and these colours and gross patterns are reasonably consistent within a species, i.e. one individual looks like another (Harper 1978). However, it is also known that in many species of Aves plumage changes with age and breeding condition, and between sexes (Van Tyne & Berger 1976). In any systematic examination of plumage differences among populations of the same or closely related species of seabirds two factors are very important – age and sex. These factors were not available for this study, and thus we can draw only limited conclusions. We can say, however, that if systematic changes with age (or any other factor) occurred in both collar and forehead patterns for Dark-rumped Petrels, the coincident changes would be manifested as a correlation between these patterns. No correlation was found.

Plumage is the easiest character to observe and quantify in the field, and has played an important role in separating populations of seabirds, e.g. *P. rostrata, P. arminjoniana, P. hasisata, P. longrostris, P. leucoptera, Diomedea epomophera, D. cauta,* (Tuck & Heinzel 1978), *P. mollis* (Clancey *et al.* 1981). Plumage, like breeding habitat and vocalisations, should be included in any comparisons between populations of similar birds: thus a more detailed investigation of plumage of Dark-rumped Petrels in Galapagos is necessary, and it must take into account age and sex, i.e. it must deal with known-age birds.

Vocalisations

Simons (1985) reported that Dark-rumped Petrels in Hawaii use two predominant calls, a "penetrating, resonant" call and a "similar but ... raspy and nasal rather than resonant" call, but he did not ascribe the difference in sound to sexual dimorphism. We cannot prove sexual dimorphism in calls because we do not know the sex of recorded birds. However, based on the findings of others for other petrels (Grant *et al.* 1983, James & Robertson 1985), we assume that the Sweet calls are made by males and the Coarse calls by females. Sexual dimorphism in this species will be investigated more intensively (S. Kress, pers. comm.) during current research on attraction and colonisation (Kress[7]).

The sound and quality of all syllables differed greatly between the sexes. Females (Coarse) seemed to modulate frequency and amplitude rapidly in all syllables, whereas males (Sweet) seemed to produce a pure tone (i.e. without frequency or amplitude modulation) for DRONE syllables. The male long call

[7] S. W. Kress, Egg Rock Undate, 1988 Report.

in Fig. 3 shows that the second and third syllables overlap slightly in time. Although this overlap was seen only once, and is atypical, it demonstrates that males are capable of using both internal tympanic membranes asynchronously. We presume the differences between male and female modulation are caused by each sex using the tympanic membranes differently, possibly males synchronously and females asynchronously.

Interisland separation was indicated by 14 parameters in males and seven in females; only three were common to both sexes – F1(DRONE),F1(FINAL) and T1(DRONE). The presence of a high number of interisland differences in female as well as male calls would help birds of opposite sex from the same island to identify each other. Thus, vocalisations may be a genetic isolating mechanism.

Calls recorded on one island are different from those recorded on another island. The statistical analyses that established interisland differences in vocalisations were based solely on recordings of the calls made on each island, and it was impossible to make any allowance for visiting birds. However, if the analyses do include calls of visiting birds, these calls would dilute the observed differences between islands. Thus, interisland differences in vocalisations that we have demonstrated are conservative and may understate the situation.

It is impossible to know which components of calls are the most important to the birds' identification, and possibly isolation, without experiment. It is reasonable to hypothesise that the components most consistently different throughout all or most calls, and which are statistically the most different, are indeed the most important to the birds. In male calls, these components are the basic frequency of all syllables, the time interval after most syllables, and the duration of most syllables. We suggest that one can deduce with confidence the island of origin of a male bird by examining these components of a recorded call. No such clear-cut pattern was evident for females, although the results from the few calls analysed indicate that the island of origin might also be deduced.

Frequently, a Sweet call was interrupted or closely followed by a Coarse call, or vice versa. It is possible that this sequence is produced by a bird announcing its individual identity, sex and breeding status, and being answered in kind by a bird of the opposite sex. Simons (1985) noted a similar pattern of a resonant call being answered by a raspy call in the Hawaiian subspecies. The statistical similarities of OOO and SOT syllables may indicate that both have the same function. If this is so, what function does the similarly structured FOT syllable have? It may complement the function of the SOT syllable; it seems unlikely that, in such a short unvarying call, this major component is useless.

Vocalisations are important in courtship, and in individual and specific identification by nocturnal birds that breed in large colonies and have a very similar overall plumage pattern. Marler (1957) suggested that sympatric species maintain their specific integrity by evolving similar calls of aggression or warning, and by evolving dissimilar calls which lead directly to courtship or breeding. The most prominent syllable studied here in all Dark-rumped Petrels calls in Galapagos, the DRONE, is dissimilar among islands for males and females, and so may contribute significantly to genetic isolation.

A widely accepted explanation of geographical variation and dialect is offered by Marler (1957) (called microgeographic and macrogeographic variation by Mundinger 1982), who said that geographical variation occurs over long distances among populations which do not usually interbreed, but that local dialects occur when the songs (calls in Dark-rumped Petrels) within one population are similar to, but different from other populations with which interbreeding could easily occur. We accept that explanation and suggest that the birds in Galapagos have evolved island dialects.

We assume that petrels are successful at recognising individuals from their natal island, and that they use some or all of the parameters we used. After discriminant analysis of male vocalisations, 82.2% were correctly classified into island of origin. A different sample (of unsexed birds) was used in a similar analysis of morphology, which correctly classified 58.6% of birds from five populations. A theoretical combination of these two analyses implies a potential classification rate of 92.6%. Therefore, given adequate information, we can accurately classify birds into source populations. Although most people can easily detect differences (vocalisations and sometimes plumage) between Galapagos and Hawaiian subspecies, differences among populations within the Galapagos, shown here to be statistically significant, are not so readily apparent as to warrant subspecific status.

Recent work (Cox *in* Simkin 1984) suggests that Santiago is less than 0.7 million years old, Santa Cruz and Floreana are between 0.7 and 1.5 million years old, and San Cristobal is more than 2.4 million years old. Thus, it is possible that the colonies were not established simultaneously, and at least two colonisation patterns are possible. Birds from the first island populated (probably the oldest, San Cristobal) may have subsequently colonised younger islands. Alternatively, there may have been more than one wave of colonists (e.g. EOY and MOY breeders), taking advantage of changes in climate in the last 10 000 years (Grant 1986). The newest island (Santiago) was probably colonised gradually but relatively recently by birds from other islands. This is supported by the high percentage of misclassification of Santiago birds following the morphology discriminant analysis, and the weak third discriminant function derived in the analysis of Sweet calls, which partially separates the Santiago population (Fig. 8B).

No movements between islands have been recorded during nine years of recovery of banded birds, and birds rarely move between colonies (Tomkins 1985, F. and J. Cruz, pers. comm.). Many species in this family have been shown to be highly faithful to their natal island, and this trait, regardless of where they feed, would be an effective isolating mechanism.

Once isolation exists, several evolutionary mechanisms can act on a population, e.g. founder effect, genetic drift and character displacement caused by interspecific competition (Bourne 1955, 1957, Ashmole 1963, Lack 1966). Any of these could produce the interpopulation differences in breeding phenology, morphology and vocalisations we have investigated in this study. What has caused the differences is unknown. Current population numbers in Galapagos are much smaller than those of a few decades ago. The differences we have revealed may have been typical of those large populations, or they may occur in survivors of very recent, severe habitat changes brought about by humans.

Comparisons with other species

Dark-rumped Petrels in Galapagos are significantly larger (16%) than those in Hawaii; by contrast, Hawaiian eggs are significantly larger (18%) than Galapagos eggs. Loomis (1918) details variation in plumage between Galapagos and Hawaiian birds. The most important of these differences is that the black markings of the forehead are variable among Galapagos birds, and are lacking in Hawaiian birds. Hawaiian birds lay eggs over a period of about four weeks (Simons 1985) in the Northern Hemisphere summer, when the weather is relatively dry and cool. In contrast, eggs are laid in Galapagos during at least 10 months of the year, in the wet cool winter and the humid hot summer. But the most outstanding feature is the difference in vocalisations recorded over breeding colonies. The sonagrams of Dark-rumped Petrel calls in Hawaii (Simons 1985, Tomkins, unpubl. data) are very different from those in Galapagos. Dark-rumped Petrels in Galapagos and Hawaii may be more distant taxonomically than currently recognised. They differ in many aspects (morphology, plumage, breeding timetable and habitat, and vocalisations), and considering the similarity in gross plumage and vocal patterns of their congeners, they may be different species. There is no evidence that birds from Galapagos and Hawaii interbreed, and the commonly held view that birds from Hawaii as well as Galapagos feed in the eastern tropical Pacific Ocean (Tuck & Heinzel 1978) needs review. Considering the results of this present study, it may be that Hawaiian birds had similar interpopulation differences. Historically they bred on all the main Hawaiian islands (Munro 1944), but now they have been so reduced that breeding has been confirmed on only one island (Simons 1985).

The calls of the other members of the *P. hasitata* superspecies vary greatly within the group, and this makes selection of analogous calls difficult. Calls selected at LNS for comparison were so different from those of the Dark-rumped Petrels in Galapagos that statistical treatment was unnecessary. *P. p. phaeopygia* is dissimilar to other members of the superspecies, whereas *P. p. sandwichensis* is similar to *P. cahow* and *P. hasitata* (this study; King, pers. comm.).

Members of the *P. hasitata* superspecies have many similarities, and yet their calls are for the most part different. Vocalisations should make a major contribution to *Pterodroma* taxonomy because, as Meredith[2] pointed out, "(*Pterodroma*) genus ... classification ... is based on subtle shape variation ... as there are no major differences (in morphology) to be found".

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