Variation in the size and shape of Darwin's finches

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Six bill dimensions, and wing, tarsus and hallux lengths were measured on almost all museum specimens of *Geospiza* species available, and up to 20 specimens from each population of the remaining species of Darwin's finches. The data were subjected to univariate and multivariate analyses in order to provide a quantitative description of size and shape differences among populations and between species.

Each species of *Geospiza* varies among islands in size, and most of the remaining species do so as well. There is more variation in shape among species than among populations of the same species, especially in bill proportions. Allometric relations differ among species. Approximate morphological counterparts to the ground finch species, *Geospiza*, can be identified among the tree finches. There is a small amount of overlap in multivariate space between a ground finch species and a tree finch species (two cases), but no overlap between any two species within each group. Size variation among populations is not generally correlated with geographical variables such as latitude, longitude, island area or its degree of isolation. Nor do coefficients of variation show strong geographical trends. Several of the results confirm the findings of other workers from simpler and non-statistical comparisons. In addition we have shown that the tree finches have relatively long legs (tarsi), and that these finches as well as the ground finches which spend most time scratching on the ground or climbing in cacti also have a relatively long hallux (hind toe). To interpret the various morphological patterns a knowledge is required of inter-island variation in food supply, feeding habits and the incidence of genetic exchange between populations. Recent field studies have provided some of this needed information, which helps to explain, among other things, why several populations of Darwin's finches are so unusually variable.

KEYWORDS:—Size – shape – coefficient of variation – allometry – multivariate analysis – geographical trends – differentation – isolation – Galápagos.

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INTRODUCTION

Until recently, our understanding of the adaptive radiation of Darwin's finches was derived almost entirely from morphological studies. Swarth (1931, 1934) and Lack (1945, 1947) described the major patterns of morphological differentiation, and Bowman (1961) investigated many aspects of the functional anatomy of the finches. In contrast to the precise details of morphology, the ecological features of the finches were known only in general and qualitative terms. In the last 12 years this situation has been rectified through intensive investigations of the feeding, breeding and demography of several species on the Galápagos islands (Grant, 1984). In the course of this work questions have arisen concerning the significance of size and shape variation that cannot be answered by the results of earlier morphological studies (e.g. Grant *et al.*, 1976; Abbott *et al.*, 1977). Consequently we have undertaken a more comprehensive morphological study of museum specimens of Darwin's finches, and this paper presents our results.

Lack (1945, 1947) restricted his attention to three dimensions; wing length, bill length and bill depth. He characterized populations in terms of their means and standard deviations, ratios of means, and to a lesser extent by coefficients of variation and parametric correlation coefficients. In the present study we examined almost all specimens examined by Lack, and some others, we measured nine dimensions on each specimen, performed univariate and multivariate computations, and investigated allometric relations among populations of the same species and among species.

The results are valuable in providing a more comprehensive characterization of size and shape variation within and among Darwin's finch species than currently exists. They are also useful in answering specific ecological and evolutionary questions that require a knowledge of the relationship between morphological and ecological characteristics of individuals or species (e.g. Grant, 1981a, 1983; Grant & Schluter, 1984; Price *et al.*, 1984; Price & Grant, 1984; Schluter & Grant, 1984a, b). However, in this paper we are concerned primarily with the description of morphological variation and not with explanations for the adaptive radiation.

The species, 13 on the Galápagos islands and one on Cocos island, are listed in Table 1.

Table 1. Darwin's finches

Scientific name	Abbreviations used in Figs	English name
Geospiza magnirostris	MAG	Large ground finch
Geospiza fortis	FORT	Medium ground finch
Geospiza fuliginosa	FUL	Small ground finch
Geospiza difficilis	DIFF	Sharp beaked ground finch
Geospiza scandens	SCAN	Cactus finch
Geospiza conirostris	CON	Large cactus finch
Platyspiza crassirostris	CRASS	Vegetarian finch
Camarhynchus psittacula	PSIT	Large tree finch
Camarhynchus pauper	PAU	Medium tree finch
Camarhynchus parvulus	PARV	Small tree finch
Cactospiza pallida	PAL	Woodpecker finch
Cactospiza heliobates	HEL	Mangrove finch
Certhidea olivacea	OL	Warbler finch
Pinaroloxias inornata	IN	Cocos finch

Scientific names follow Bowman (1961: 20), English names follow Lack (1947: 18) but are simplified by deletion of hyphens. For further comments see Appendix.

METHODS

Specimens in juvenal plumage were ignored, and nine dimensions were measured on all of the remainder as follows: *wing length*, from carpal joint to the tip of the longest primary; *tarsus length*, from tibiotarsal joint to a distal, identifiable, undivided scute; *hallux*, from the base of the hind toe on the plantar surface of the foot to the base of the toe nail; *upper bill length*, from the anterior edge of the nostril to the tip of the upper mandible; *lower bill length*, from base to tip in the median plane; *upper bill depth*, from edge to maximum height in the vertical plane level with the anterior edge of the nares; *lower bill depth*, in the same plane as the previous measurement; *upper bill width*, at right angles to upper bill depth; *lower bill width*, at the base of the lower mandible at the junction with the feathers. Wing length was measured to the nearest mm with a ruler. All other measurements were taken to the nearest 0.1 mm with callipers (depths and widths) or dividers.

The study was restricted to the *Geospiza* species when initiated in 1973, and we measured almost all specimens available, a total of 5812. Measurements were made by I.A. except for those on 50 specimens made by P.R.G. after standardization of methods. The study was extended in 1977 to the remaining species (tree finches and warbler finch), but not more than 20 specimens of each population were measured, for a total of 780. Measurements were made by P.R.G. and R.L.C., again after standardization. Only the measurement of hallux length was difficult to standardize. Inadvertently we measured tarsus length differently in the two groups; the distal point was taken to be one scute closer to the foot on the other finches than on the ground finches (*Geospiza*). Therefore we measured a few specimens of each of the tree finch and warbler finch species a second time to calculate a correction factor which was then applied in order to make comparisons with the ground finches.

Analyses were performed on the MIDAS computing system at the University of Michigan, and the details are given in the Results section. Unless stated explicitly, statistically significant differences refer to $P < 0.05$. Univariate

analyses were largely restricted to the *Geospiza* species (Appendix Tables), but all species were subjected to multivariate analyses.

We performed one methodological check on the reproducibility of the results. I.A. measured 17 specimens of *Geospiza fuliginosa* twice, about 1 h apart. The species was chosen because it is the smallest *Geospiza* species and therefore measurement error is likely to be relatively large. Correspondence between the two sets of measurements was generally good (Table 2), and needs only a few comments.

There were no significant differences in means or variances between first and second sets of measurements ($P > 0.1$ in each case). Means were within 1% of each other, except for upper mandible depth (1.4%); this is comparable to results from other studies (e.g. Grant, 1979). Repeatabilities are all very high, as high as or higher than estimates obtained from live birds on the Galápagos (Boag, 1983; Grant, 1983; Price & Grant, 1984). Correspondences between first and second measurements are also shown by parametric correlations, and by the proportion of the 17 specimens which yielded identical first and second measurements of a trait, which we refer to as accuracy. Accuracy was highest for upper mandible length, as was repeatability, and lowest for lower mandible depth. The low repeatability of tarsus length measurements resulted from widely discrepant values in successive measurements on two specimens. In each case one measurement was in error, probably because the wrong scute was chosen for the distal point. But the errors cancelled; one was in the first sample and the other was in the second. This example shows that occasional errors of measurement or recording may have little influence on estimates of means.

RESULTS

Morphological comparison of populations will be presented in three sections. We first consider some aspects of the frequency distributions of traits: differences

Table 2. Comparison of measurements taken twice on each of 17 specimens of *Geospiza fuliginosa* from Islas San Cristóbal and Floreana. For each dimension (mm) the smaller mean is expressed as a proportion of the larger mean to give a similarity value. Repeatability is an expression for differences (variance) among individuals as a proportion of total variance. Accuracy refers to the proportion of specimens with identical measurements in first and second samples

|	Wing	Tarsus	Hallux	Bill length		Bill depth		Bill width	
				Upper	Lower	Upper	Lower	Upper	Lower
1st mean	62.7	17.08	9.51	8.15	6.46	3.54	3.71	4.51	6.40
S.E.	0.33	0.158	0.104	0.136	0.085	0.051	0.048	0.036	0.063
2nd mean	62.2	17.07	9.56	8.11	6.47	3.49	3.69	4.48	6.36
S.E.	0.35	0.155	0.094	0.136	0.087	0.051	0.044	0.039	0.065
Similarity of means	0.993	0.999	0.995	0.995	0.998	0.986	0.995	0.993	0.994
Repeatability	0.98	0.45	0.85	0.99	0.95	0.68	0.73	0.81	0.89
Accuracy	0.59	0.53	0.35	0.65	0.35	0.35	0.29	0.47	0.47
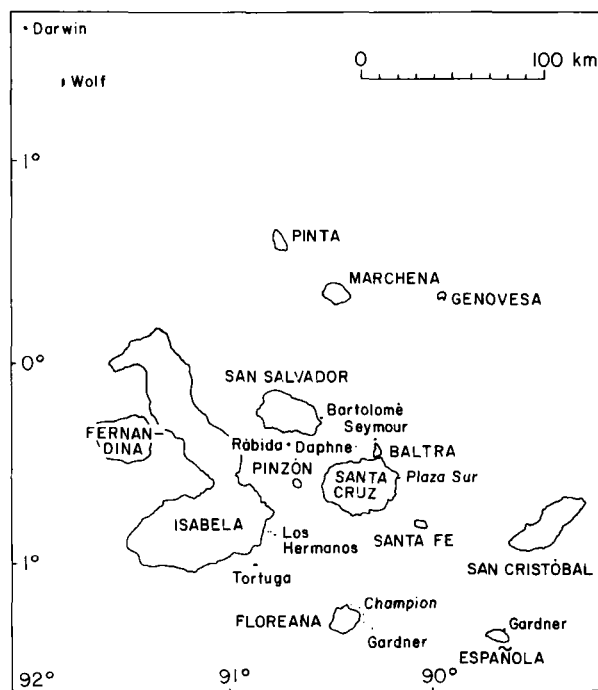
Figure 1. The Galápagos archipelago. Two islands mentioned in the Appendix are not shown: Is Enderby is between Islas Champion and Gardner near Floreana, and Is Cowley is between Islas Isabela and San Salvador but closer to Isabela. Floreana is also known as Santa María and San Salvador is also known as Santiago.

between the sexes in means; and variances, skewness and kurtosis. Next we compare size and shape variation in univariate and multivariate analyses. Finally we examine geographical trends in size and in population variation throughout the Galápagos archipelago (Fig. 1), and also specifically trends in size on small islands. Some taxonomic problems concerning nomenclature and status are discussed in the Appendix.

Frequency distributions

Sexual dimorphism

Males are consistently larger than females, by a few per cent. The degrees of dimorphism for the *Geospiza* species are shown in Table 3. Sample sizes for the remaining species are smaller, but these species appear to be no more dimorphic than the ground finches (see also Lack, 1945).

The sexes differ least in bill length, as has been found with the house sparrow, *Passer domesticus*, (Johnston & Selander, 1973). All species of ground finches are more dimorphic, on average, in wing length than in bill length or tarsus length, and are most dimorphic in bill width and bill depth.

Although *G. conirostris* is the most dimorphic species, as noted by Lack (1945, 1947) and Downhower (1976), it is not so by a large margin, nor is it so in all dimensions, and nor does it show the highest degrees of dimorphism: these are shown by *G. scandens* on Is San Salvador (lower bill depth) and on Is Pinta

Table 3. Average sexual dimorphism, expressed as the mean percentage difference between males and females for all populations of *Geospiza* species. Populations were included only if they were represented by at least 10 male and 10 female specimens. All values in the table are positive because all male means are larger than female means

Species	Number of Populations	Wing	Tarsus	Upper mandible			Lower mandible		
				Length	Depth	Width	Length	Depth	Width
magnirostris	6	3.86	2.23	2.31	4.65	3.99	1.16	4.01	3.82
fortis	11	3.67	3.21	1.54	2.46	2.80	0.64	1.45	1.93
fuliginosa	13	3.53	2.70	1.50	2.39	2.31	2.01	1.99	3.56
difficilis	5	2.87	1.75	1.33	1.57	2.56	1.37	0.92	3.31
scandens	7	3.95	3.30	2.07	2.25	3.72	1.88	4.44	5.04
conirostris	3	4.31	2.87	3.44	5.08	4.71	2.45	4.87	4.96

(lower bill depth, upper and lower bill width). The population of *G. fortis* on Is Pinzón is unusual in showing reversed dimorphism: females are larger than males on average (Price, 1984).

While the degree of sexual dimorphism is typical of small passerines in not being very pronounced, it is large enough that it needs to be allowed for in comparisons of populations or species when the sexes are unequally represented. Price (1984) has examined the variation in sexual dimorphism among populations in detail.

Variance

There is significant heterogeneity in variances among some samples. Data from just one species are used to illustrate heterogeneity in levels of variation among populations of the same species (Table 4). Coefficients of variation are used to reduce, if not to eliminate altogether, the effects of scale (see Van Valen, 1978; Rohlf *et al.*, 1983), because population means differ. Only males are used because they are larger on average than females and so should not be combined with them, and their samples are generally greater. Several populations of *G. difficilis* differ from each other in their degrees of variation in two bill dimensions (Table 4). These differences in coefficients of variation do not vary systematically with differences in means.

Table 4. F values for comparisons of male samples of *G. difficilis*, calculated from squared coefficients of variation. Two-tailed probability values are indicated by *italics* (<0.05) and **boldface** (<0.01)

Lower bill width	Upper mandible length					
	Santa Cruz	San Salvador	Genovesa	Pinta	Wolf	Darwin
Santa Cruz	—	1.59	**2.46**	*2.92*	1.59	1.15
San Salvador	1.77	—	1.55	1.84	1.00	1.38
Genovesa	1.66	1.07	—	1.19	1.54	**2.14**
Pinta	**5.14**	**2.90**	**3.09**	—	1.84	*2.54*
Wolf	1.54	1.15	1.07	**3.33**	—	1.38
Darwin	1.07	1.66	1.55	**4.81**	1.41	—

Table 5. Average coefficients of variation for male samples ($N \geqslant 10$) of *Geospiza* species, with minimum and maximum coefficients for each species shown below in *italics*. Coefficients for *Fringilla* species on Atlantic islands (Grant, 1979) and for *Carpodacus maxicanus* on Californian islands (Power, 1983) are provided for comparison. Sample sizes of original measurements are comparable in all three studies. The total bill depth was measured on *Carpodacus* specimens

	No. of populations	Upper bill length	Upper bill depth	Lower bill width
Geospiza species				
magnirostris	6	5.68	8.77	5.98
		4.76–6.25	*6.44–12.66*	*4.36–7.94*
fortis	12	6.11	10.04	7.73
		3.40–8.95	*4.38–13.84*	*3.65–10.99*
fuliginosa	16	5.36	8.65	5.24
		3.94–10.63	*6.80–14.37*	*3.16–8.17*
difficilis	6	4.66	9.55	5.73
		3.55–6.07	*7.78–11.14*	*4.21–9.54*
scandens	9	5.27	8.80	5.78
		3.62–7.04	*7.13–12.22*	*4.26–6.43*
conirostris	3	6.68	8.80	7.41
		6.06–7.21	*7.72–9.99*	*6.84–7.83*
Fringilla species				
coelebs	14	4.08	4.21	3.32
		3.38–6.76	*3.14–5.01*	*2.69–4.50*
teydea	12	2.78	3.74	2.25
		2.19–3.37	*3.72–3.76*	*2.17–2.34*
Carpodacus species				
mexicanus	4	5.02	3.59	4.14
		3.80–5.84	*3.15–5.59*	*3.17–5.10*

Species also differ from each other in their levels of variation. The bill data for *Geospiza* species are summarized in Table 5. For example, the average coefficient of variation for upper bill length is significantly greater in *G. conirostris* than in *G. difficilis* ($t_7 = 3.22$; $P < 0.002$). In general, species with largest means have the largest coefficients of variation (see also Grant *et al.*, 1976; Abbott *et al.*, 1977). The average coefficients of variation confirm Lack's (1947) finding that *G. fortis* is the most variable species, on average. However, it is not the largest species.

The coefficients for bill length and depth are higher than those reported by Bowman (1961) from Lack's data, because Lack's samples were restricted to male specimens in fully black plumage, whereas ours include all males. Even so, when we excluded specimens in brown plumage and reanalysed just bill depth data we found almost as many increases (23) in the resulting coefficients of variation as decreases (25). Lack measured total bill depth which, being larger, should be subject to smaller measurement error than measurements of each mandible separately. Note that coefficients are generally much larger in the ground finches than in island populations of other finch species (Table 5) that have been studied in similar detail.

Dimensions covary positively. A population with a large average wing length, for example, tends to have large average tarsus and bill dimensions as well. Similarly, coefficients of variation in a population tend to be relatively large, or

relatively small, for all dimensions. Covariation is demonstrated by the numerous positive correlations among traits within populations, and by large Kendall coefficients of concordance, W (Sokal & Rohlf, 1981), calculated separately for means and for coefficients of variation. As tested by χ^2, in each of the six *Geospiza* species there is significant concordance among populations in the relative size of traits; this applies to males and females, treated separately. The same result is obtained for coefficients of variation. Here only males were tested. The one exception is *G. conirostris* ($W = 0.26$; $\chi_2^2 = 4.67$; $0.05 < P < 0.1$). But this species is not exceptional when the analysis is restricted to the six beak variates ($W = 0.78$; $\chi_2^2 = 9.33$; $P < 0.01$).

Skewness

Samples of 25 individuals or more of either sex were tested for skewness following the procedure of Snedecor & Cochran (1967). Five-hundred-and-sixty tests were performed: eight traits (hallux excluded) in 70 samples. Five per cent of these (28) would be expected to yield a significant departure from normality at $P < 0.05$. In fact 113 were significant at this level. Male and female distributions were skewed with approximately equal frequency, in both directions.

The high number of skewed distributions is partly explained by the prevalence of positive correlations and concordance among all traits in all species. As a result, a skewed distribution in one trait is likely to be accompanied by a skewed distribution in the same direction in other traits. A test that circumvents this problem of dependence is a comparison of the incidence of significant skewness in each dimension with the random expectation of 5% of 70 (samples), i.e. 3.5. Measured against this expectation, distributions are much more often skewed than expected by chance (Table 6).

There is significant heterogeneity among the species in the frequency of positive and negative skewness ($\chi_5^2 = 23.56$; $P < 0.001$). Individually, two species show significant heterogeneity among skewed samples. *G. fortis* samples ($N = 12$) that have skewed distributions are predominantly positively skewed (Binomial test, 2-tailed; $P = 0.06$) whereas the trend is opposite for *G. fuliginosa* samples ($N = 15$; $P = 0.006$).

Kurtosis

Samples of 11 individuals or more of either sex were tested for kurtosis (see Snedecor & Cochran, 1967). The main results (Table 6) are, first kurtosis is much more frequent than expected by chance (at the 5% level), second it is more frequent than skewness, and third flat-topped distributions (platykurtosis) predominate. Unlike skewness, there is no heterogeneity among species in the directions of kurtosis.

Three systematic forces could contribute to these trends in variance, skewness and kurtosis; they are natural selection, growth and hybridization. Since the samples are composites of subsamples taken in different years they could be annually heterogeneous. Different selection episodes in different years could be responsible for annual differences in mean size (cf. Boag & Grant, 1981). Alternatively size-related age compositions might vary from year to year and distort the frequency distributions in different directions. The same effect could be produced by varying frequencies of hybridization, although the directions of

Table 6. The number of samples of *Geospiza* species with significant ($P < 0.05$) skewness or kurtosis. Positive kurtosis is leptokurtosis and negative kurotosis is platykurtosis; note the predominance of negative kurtosis

	Wing	Tarsus	Bill length		Bill depth		Bill width			Summary	
			Upper	Lower	Upper	Lower	Upper	Lower		Skewness	Kurtosis
Skewness									Only negative	24	45
Positive	3	3	6	9	4	10	9	10	Only positive	12	12
Negative	5	7	10	5	16	3	5	5	Both	8	19
Total	8	10	16	14	20	13	14	15	Neither	26	20
									Total	70	94
Kurtosis											
Positive	4	3	5	5	6	3	3	2			
Negative	13	17	21	15	11	14	18	22			
Total	17	20	26	20	17	17	21	24			

skewness in the (small) *G. fuliginosa* and the (medium) *G. fortis* are the opposite of those expected from an hypothesis of hybridization between them. Either singly or together these factors could give rise to composite distributions that depart from normality in any of the observed ways. However, these distortions are not likely to have major effects on the estimates of variances (or means), as indicated by the good agreement between estimates derived from measurements of live birds over periods of a few weeks or months and estimates based on measurements of composite samples of museum specimens; compare coefficients of variation in Abbott *et al.* (1977), Grant & Grant (1979, 1983) and Boag & Grant (1984a, b) with values in Table 5 or those published in Lack (1945) or Bowman (1961).

Size

There are two ways to measure size, by weighing birds and by measuring dimensions. Some weights have become available in recent years in the course of ecological field studies, and they are summarized in Table 7. Each *Geospiza* species varies in mean weight significantly ($P \ll 0.05$) among islands (ANOVAS). The most variable species is *G. difficilis*: average weights of males range from 11.6 g on Genovesa to 26.8 g on San Salvador. Marked and consistent differences between species are also evident in Table 7.

Table 7. The mean weights of males in partially or wholly black plumage in the dry season. Sample sizes are in parentheses. Data are from several field studies: Smith *et al.* (1978), Grant & Grant (1980), Schluter (1982), Schluter & Grant (1984b), Boag & Grant (1984b) and unpublished. B. Borrero is on the north side of Is Santa Cruz, and B. Academía is on the south side

Island	*Geospiza* species					
	magnirostris	*fortis*	*fuliginosa*	*difficilis*	*scandens*	*conirostris*
Pinta	36.9 (18)	17.7 (11)	11.3 (72)	19.0 (23)	23.0 (12)	
Marchena	32.6 (12)	17.4 (4)	9.7 (11)		23.8 (2)	
Genovesa	35.5 (27)			11.6 (56)		25.3 (26)
Wolf				20.5 (22)		
Darwin				25.5 (4)		
San Salvador	39.0 (5)	20.7 (8)	14.7 (30)	26.8 (13)		
Fernandina	28.9 (3)	19.6 (5)	12.7 (15)	19.6 (11)		
Tortuga			16.0 (12)			
Española			14.6 (16)			31.6 (19)
Daphne		16.5 (82)			21.6 (30)	
B. Borrero		19.6 (20)	13.2 (24)		20.4 (5)	
B. Academía		23.0 (62)	14.1 (9)		22.6 (6)	
Santa Fe			13.1 (5)		20.3 (5)	
Hermanos			16.5 (2)			
Champion		21.4 (4)			21.4 (6)	
Isabela		19.4 (18)	14.5 (17)			
Rábida	34.0 (4)		14.2 (21)		21.5 (8)	
Gardner			14.6 (16)			27.6 (10)

Additional mean weights of tree finches, sexes combined: *Platyspiza crassirostris* 34.7 (2; Santa Cruz); 29.3 (12; Pinta); 33.9 (4; San Salvador): *Cactospiza pallida* 20.2 (3; Santa Cruz): *Camarhynchus psittacula* 17.2 (2; Santa Cruz); 19.4 (7; Pinta): *Camarhynchus parvulus* 12.8 (81; Santa Cruz): *Certhidea olivacea* 9.3 (14; Santa Cruz); 8.8 (13; Pinta); 8.3 (8; Genovesa); 7.9 (7; Española); 8.9 (9; Gardner by Española); 8.8 (3; Hermanos).

Table 8. Parametric correlation coefficients between mean weight and mean dimensions of male samples of *Geospiza* species. Mean weights are listed in Table 7

Geospiza species	No. of populations	Dimensions		
		Wing length	Tarsus length	Bill length
magnirostris	5	0.19	0.23	0.59
fortis	8	0.79*	0.79*	0.73*
fuliginosa	11	0.90**	0.87**	0.80**
difficilis	6	0.81*	0.92**	0.66
scandens	7	0.35	0.41	0.52

Statistically significant correlations are indicated by *$P < 0.05$; **$P < 0.01$.

All measured traits covary positively in the largest samples of museum specimens. Which trait has the strongest relationship to weight? An analysis of population means shows that wing and tarsus are generally correlated more strongly with weight than are bill dimensions, but by not much. Table 8 gives the results of separate analyses for each *Geospiza* species. The same result is obtained when all *Geospiza* species are considered simultaneously (Fig. 2). Correlation coefficients are high for the relationship between weight and wing ($r = 0.96$; d.f. $= 38$; $P < 0.001$) and between weight and tarsus ($r = 0.96$; d.f. $= 38$; $P < 0.001$); wing and tarsus are also strongly correlated with each other ($r = 0.97$; d.f. $= 38$; $P < 0.001$; see also Fig. 3). The slopes of the functional regressions (see Harvey & Mace, 1982) of wing or tarsus on weight with ln-transformed data are also similar to each other: 0.286 for wing and 0.252 for
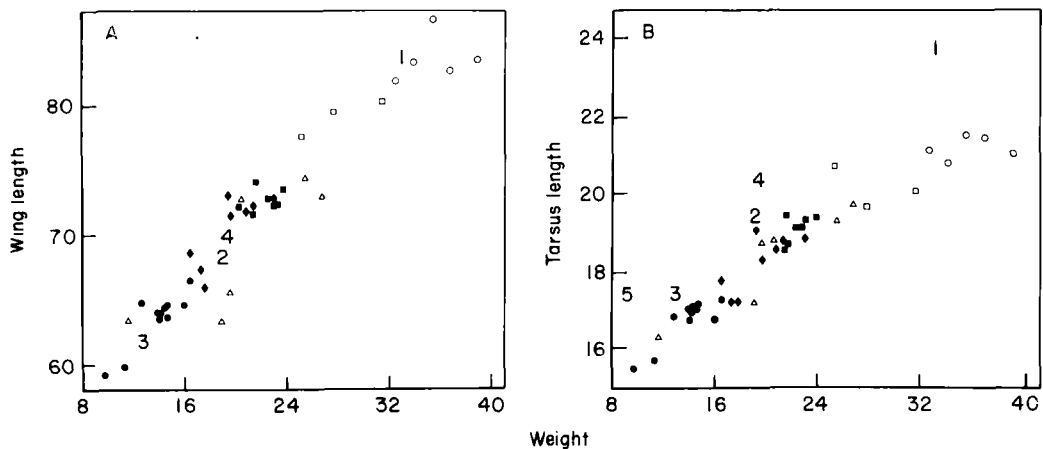

Figure 2. A, mean wing length (mm), and B, tarsus length (mm), as functions of mean weight (g) for adult male samples of *G. magnirostris* (○), *G. conirostris* (□), *G. difficilis* (△), *G. scandens* (■), *G. fortis* (◆) and *G. fuliginosa* (●). Numbers refer to the average values of tree finch species, male and females combined; 1, *Platyspoza crassirostris*;; *Camarhynchus psittacula*; 3, *C. parvulus*; 4, *Cactospiza pallida*; 5, *Certhidea olivacea*. Note the similarity of ground finches and tree finches in A, but the proportionately longer tarsi of tree finches in B. *Certhidea olivacea*, not shown in A, has a mean wing length of 53.2 mm.
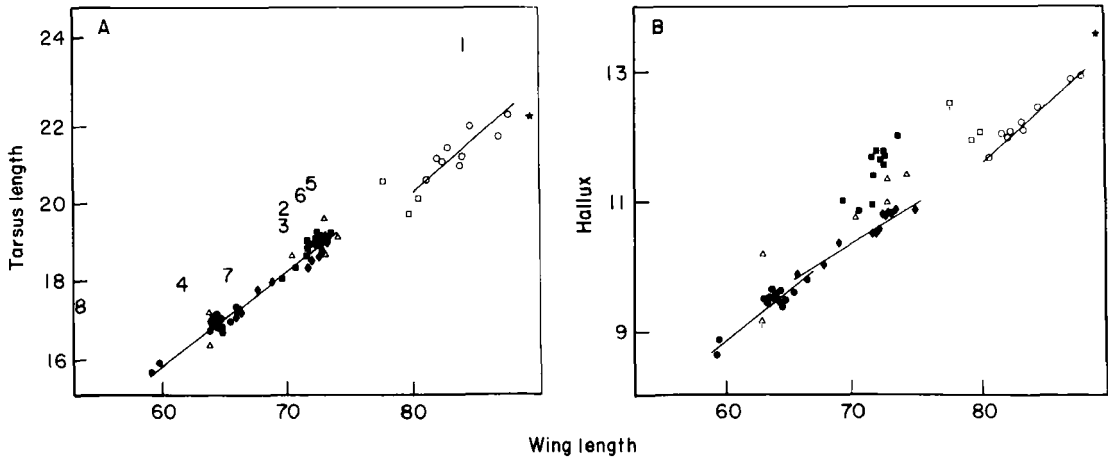
Figure 3. A, mean tarsus length (mm), and B, hallux (mm), in relation to wing length for male samples. Symbols: ○, *G. magnirostris*; □, *G. conirostris*; △, *G. difficilis*; ■, *G. scandens*; ◆, *G. fortis*; ●, *G. fuliginosa*. Functional regression lines are drawn through the population means of *G. magnirostris* (○), *G. fortis* (◆) and *G. fuliginosa* (●). Numbers: 1, *Platyspiza crassirostris*; 2, *Camarhynchus psittacula*; 3, *C. pauper*; 4, *C. parvulus*; 5, *Cactospiza pallida*; 6, *C. heliobates*; 7, *Pinaroloxias inornata*; 8, *Certhidea olivacea*. Tree finches are not included on B because hallux length may not have been measured in the same way on these and ground finches (see text). The exinct populations of *G. magnirostris* on Islas Floreana and San Cristóbal (combined) are identified by a star. Vertical lines beneath symbols identify populations of *G. conirostris* and *G. difficilis* on Is Genovesa (see text for further details).

tarsus. Therefore either wing or tarsus serves as a good indicator of size in comparisons of populations of the same or different species.

Variation in size among several correlated dimensions can also be characterized by the first component in a Principal Components Analysis (e.g. see Gould & Johnston, 1972). The analysis is useful for characterizing shape variation simultaneously, and we employ and discuss it below.

Shape

Although size variation predominates among populations there are shape differences among species. Shape changes in relation to size in a different manner among the species. Simple bivariate plots illustrate the main differences (Figs 3 & 4).

A striking difference in proportions among species is shown in Fig. 3. Although hallux increases in length as body size increases among populations, for a given body size hallux is distinctly longer in *G. difficilis*, *G. scandens* and *G. conirostris* than in the other three species of ground finches. *G. scandens*, the species which spends most time perched or climbing on cactus, has proportionately the longest hallux. The population of *G. conirostris* on Is Genovesa is a similar cactus specialist (Grant & Grant, 1981, 1982), and it has the longest relative hallux for its species. *G. difficilis* forages mainly on the ground, scratching in the litter with its feet (Schulter, 1982). The population of *G. difficilis* that does this to the least amount is on Is Genovesa, and it has the shortest hallux both absolutely and relatively (Fig. 3). Thus the hallux is well
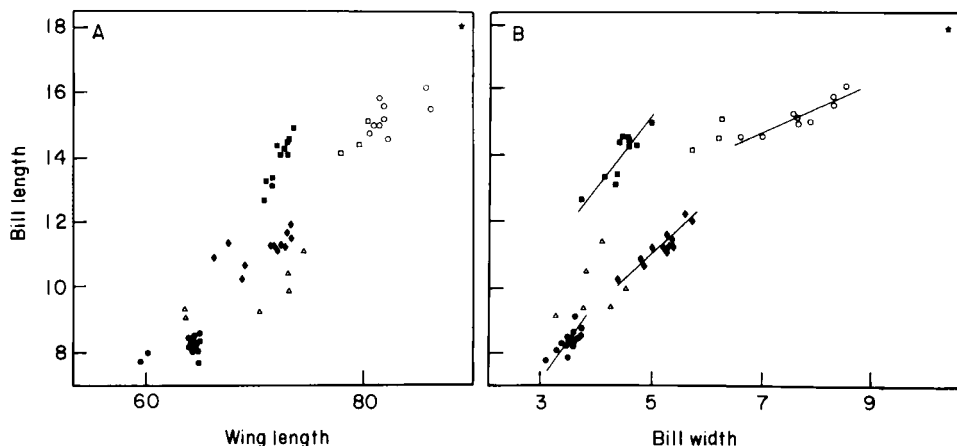
Figure 4. A, mean bill length (mm) in relation to mean wing length (mm); B, mean bill length in relation to mean bill width (mm) for male samples. Symbols: ○, *G. magnirostris*; □, *G. conirostris*; △, *G. difficilis*; ■, *G. scandens*; ◆, *G. fortis*; ●, *G. fuliginosa*. Functional regression lines have been drawn through the population means of four species in B. In B (only) the *G. magnirostris* point closest to the *G. conirostris* cluster represents the Is Darwin sample (see also the Appendix and Fig. 8). The extinct populations of *G. magnirostris* on Isla Floreana and San Cristóbal (combined) are identified by a star.

developed in those ground finches that climb or scratch on the ground most frequently.

All tree finches have long tarsi relative to body weight, but not long (or short) wings relative to body weight (Fig. 2). Therefore wing length is an appropriate size measure to use as a standard for comparison of other body parts. The hallux is relatively long in the two species of tree finch that most frequently cling to trunks and large branches, *Camarhynchus psittacula* and *Cactospiza pallida*. It is relatively short in all of the rest, but comparisons with ground finches may not be reliable because of possible measurement differences (p. 3). Nevertheless it is clear that tree finches and ground finches differ in hind limb length in relation to body size.

Within the ground finches the most notable shape variation is in the bill. Bill length does not scale in a simple manner to body size within the genus (Fig. 4A): mean bill lengths of the six species do not lie on a single straight line, and bill length increases with body size faster in some species, such as *G. scandens*, than in others, such as *G. fortis*. Also, species differ from each other most in bill shape (Fig. 4B): again all points for the six species do not lie on a single line of allometry, and bill shape changes differently among populations of the different species. Bill shape variation is also pronounced among the tree finches (see below).

Since much of the variation in proportions accompanies variation in size, it is desirable to assess the amount of shape variation that remains after the effects of size variation have been removed. This can be accomplished by Principal Components Analysis; if the first component adequately characterizes size variation, subsequent components represent residual shape variation (Flessa & Bray, 1977). Such variation is therefore largely, if not entirely (Mosimann & James, 1979; Humphries *et al.*, 1981), independent of size.

We first use PCA to describe trends of variation among individuals within

populations of species. The 14 species were subjected separately to PCA in the following way. First hallux was excluded because of a relatively low repeatability between measures. We simplified the data further by excluding lower bill length and upper bill width, and by combining upper and lower bill depth; thus one length, depth and width measure of the bill was used. All data were ln-transformed before computation. Sexes were pooled within populations. To minimize the effects of outliers on estimates of variance-covariance we then deleted the individuals with the minimum and maximum values for each trait. Finally, for each species, populations were pooled across islands to increase sample sizes. Principal components were calculated from the variance-covariance matrix.

The first two components together account for 63.6% (*Geospiza difficilis*) to 86.4% (*Camarhynchus pauper*) of the variance among individuals. The magnitude of factor loadings (Fig. 5) on the first two principal components show the relative contribution to the major synthetic axes made by the particular dimensions.

The main results are, (1) almost all factor loadings on PC1 are positive, and (2) factor loadings of wing and tarsus on PC2 are almost all positive but those for bill dimensions are always of mixed sign. The first result supports our interpretation of PC1 as an overall size axis, as does the similarity of factor

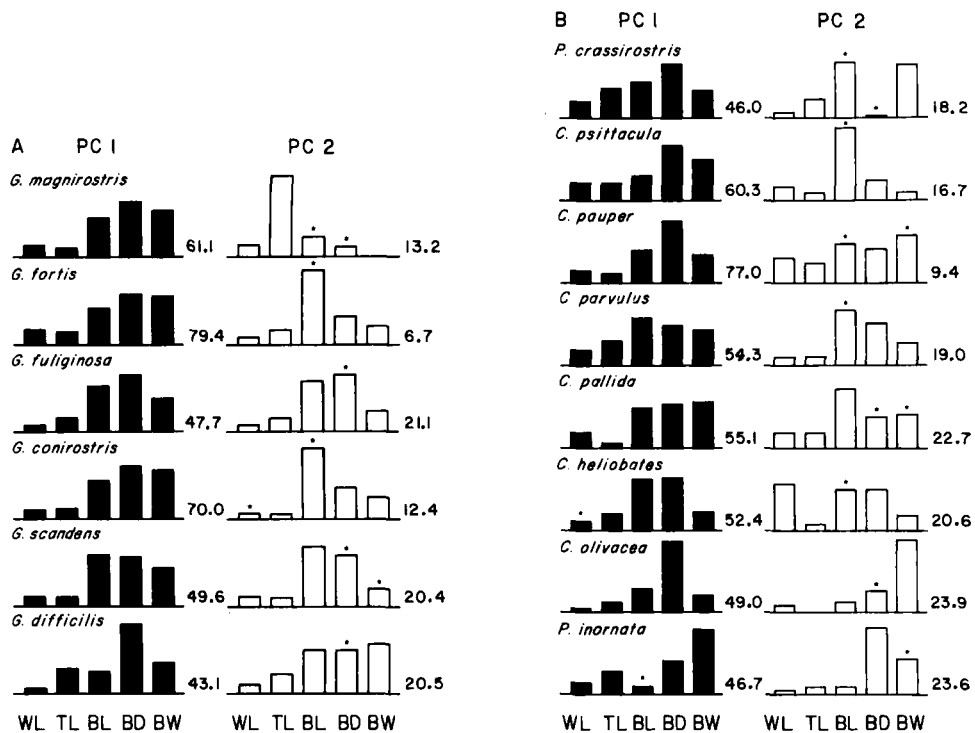Figure 5. Factor loadings on the first two principal components based on individuals within populations. The scale from 0 to 100 is shown at the bottom of the figure, and the percentage variance explained by each component is shown at the right of each histogram. Negative loadings are indicated by an asterisk. Symbols: WL, wing length; TL, tarsus length; BL, bill length; BD, bill depth; BW, bill width.

loadings on PC1 among the species (cf. Mosimann & James, 1979; 455). We interpret PC2 as a shape axis dominated by bill proportions. The importance of bill proportions is consistent with the patterns revealed by the bivariate analyses (Figs 3 & 4).

These interpretations apply to both the ground finch group and the tree finch group. In both groups bill depth is usually the greatest contributor to PC1, and bill length is the commonest major contributor to PC2. Relative factor loadings for the five dimensions are very uniform among species in the two groups. There are low values for the least variable ones, wing and tarsus, and high ones for the three bill dimensions.

Species differ among each other most in bill shape relations, as indicated by the greater heterogeneity in factor loadings on PC2, even though some individual pairs of species such as *G. fortis* and *G. conirostris* are very similar. There are no consistent shape differences between the ground finch group of species and the tree finch group. The most different pair of species are *Certhidea olivacea* and *Pinaroloxias inornata*, which are the two species with the proportionately longest beaks: bill depth and bill width dominate both axes, although in opposite ways. However, variation in *P. inornata* is estimated from only 20 specimens, which is inadequate because samples of about 50 or more are normally required for stability of covariances (Kunkel *et al.*, 1980). This species and the other two represented by small samples (*Camarhynchus pauper* and *Cactospiza heliobates*) are included in Fig. 5 for completeness.

To compare species on the same axes, we next performed a principal components analysis with separate populations of each species, i.e. not pooled. For this analysis the averages of the unscaled male and female means for each trait except hallux in each population were used, and ln-transformed prior to computation. The major trends of variation among populations and species are shown in Fig. 6. The first two components, constituted in a similar way to those in the previous analyses, account for 96.5% of the total variance. The factor loadings are similar to those from the previous analyses, except that upper mandible length and lower mandible length more clearly make the greatest contribution to PC2 (Table 9). PC1 is again a size axis; mean PC1 scores of 11 of the species are positively correlated with their average weights calculated from the data in Table 7 ($r = 0.91$; d.f. $= 9$; $P < 0.01$).

Figure 6 shows that all species are well separated in two-dimensional space, with overlap occurring between one ground finch and one tree finch species in two cases, but never between species in the same group. Separation between the two groups occurs more along the beak shape axis (PC2) than along the size axis (PC1); for a given body size (PC1), tree finches and ground finches have different bill proportions. But the two groups do not cluster in different parts of the two-dimensional plot: there is broad overlap among them.

Separate treatment of the two groups of finches (Fig. 7) provides a way of illuminating another feature of Fig. 6: that is, most ground finch species have counterparts in the tree finch group as represented in these two-dimensional characterizations. Thus there is a good correspondence between *G. magnirostris* and *Platyspiza crassirostris*; between *G. scandens* and *Cactospiza pallida*; between *G. fuliginosa* and *Camarhynchus parvulus*; and between *G. fortis* and *G. conirostris* combined and *Camarhynchus psittacula*. Only *G. difficilis* does not have a tree finch counterpart. The two species with thin pointed bills missing from Fig. 7B,
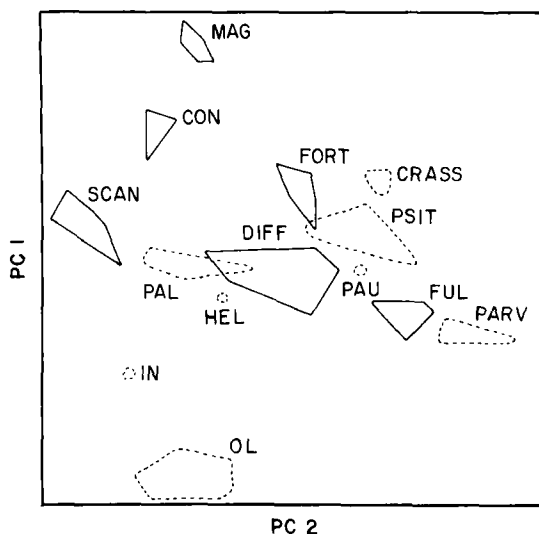
Figure 6. Principal components plot of all 14 species, based on population means. PC1 accounts for 90.4% of the variance among populations and species, and represents body size increasing away from the origin. PC2 accounts for an additional 6.1% of the variance, and represents bill shape that becomes relatively short and deep in progression away from the origin. Minimum area polyhedra are drawn around the population points for each species. See Table 1 for explanation of abbreviations.

Certhidea olivacea and *Pinaroloxias inornata*, are not the counterparts of *G. difficilis* (see Fig. 7C). The synthetic axes of Figs 6 & 7 being compared do not differ very much, nor do the factor loadings (Table 9).

Figure 7 also shows that within each group of finches (tree, ground) the orientation of intraspecific, cross-population, axes of variation are similar. But in neither group is major interspecific variation a simple extension of major intraspecific (interpopulation) variation. The closest to such a simple extrapolation is shown by the sequence of three *Geospiza* species of increasing size; *fuliginosa*, *fortis* and *magnirostris* (see also Grant, 1981b; Price *et al.*, 1984).

Table 9. Factor loadings on the first two principal components obtained for the analyses depicted in Figs 6A and 7B–D

	PC1				PC2			
	A	B	C	D	A	B	C	D
Wing length	0.152	0.149	0.247	0.188	0.009	−0.080	0.005	0.166
Tarsus length	0.049	0.119	0.255	0.122	−0.017	−0.100	0.045	0.141
Upper bill length	0.229	0.340	0.281	0.137	−0.632	−0.596	−0.617	0.668
Lower bill length	0.179	0.317	0.192	0.053	−0.707	−0.605	−0.692	0.689
Upper bill depth	0.464	0.441	0.368	0.498	0.138	0.165	0.053	−0.120
Lower bill depth	0.620	0.494	0.546	0.624	0.278	0.399	0.321	−0.174
Upper bill width	0.353	0.352	0.377	0.366	0.044	0.111	0.076	0.012
Lower bill width	0.408	0.434	0.428	0.395	0.053	0.251	0.163	0.009
Percentage variance (cumulative)	90.4	90.8	79.6	94.9	96.5	98.9	95.5	98.4

A, all finches; B, ground finches; C, tree finches, excluding *Certhidea* and *Pinaroloxias*; D, all tree finches.
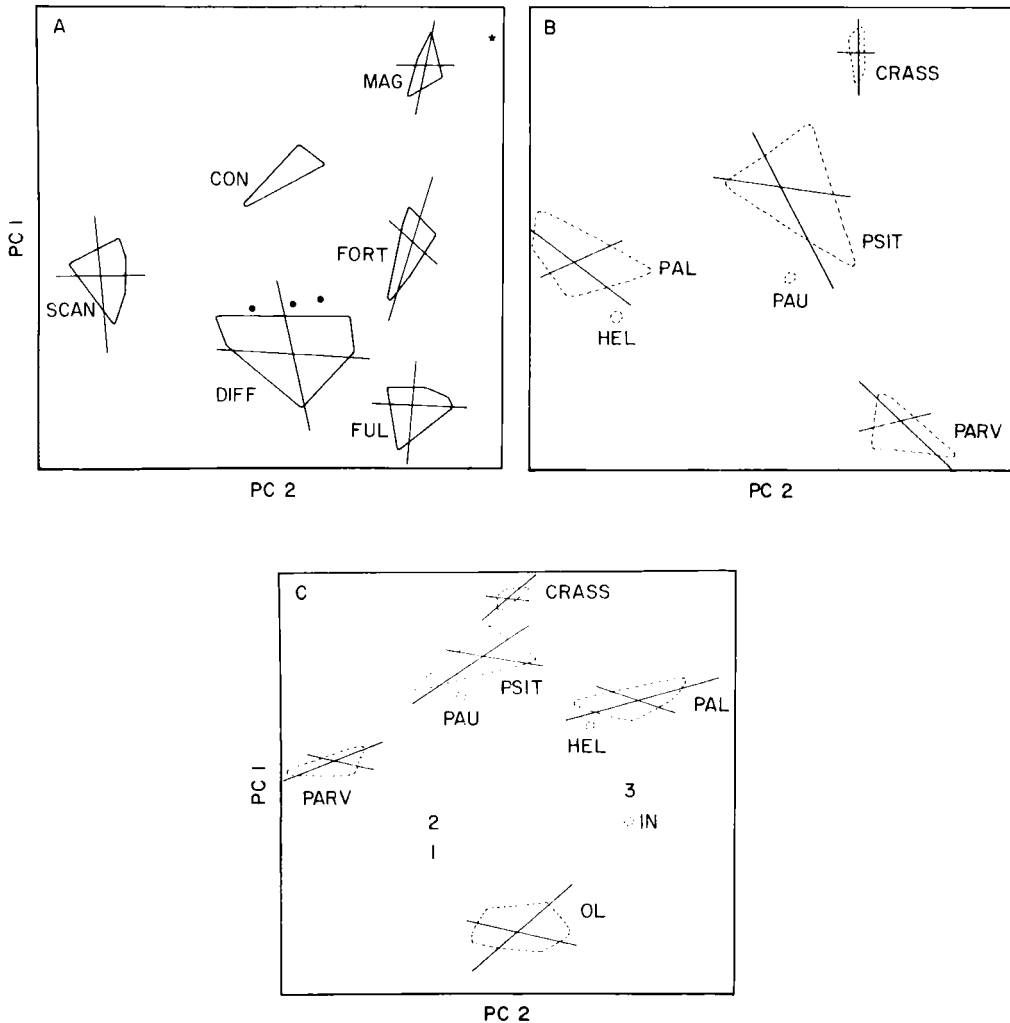
Figure 7. Principal components plot for A, ground finches, B, tree finches except for *Certhidea olivacea* and *Pinaroloxias inornata* and C, all tree finches. Lines are projections of the separate interpopulation (intraspecific) principal components 1 and 2 onto the principal components axes for all species combined; the longer lines represent PC1, being approximately vertical in A, sloping upwards to the left in B and upwards to the right in C. Cumulative percentage variance explained by the two interpopulation components ranges from 87% (*Certhidea olivacea*) to almost 100% (*Camarhynchus psittacula*). Factor loadings on the components in the three plots are listed in Table 9. The solid circles identify three specimens of *G. difficilis* from Is Floreana, which were not used in the analysis: the left two are female specimens in the British Museum and the right is a male in the Royal Stockholm Museum (see also the Appendix). The star identifies the sample of four male specimens of the extinct form of *G. magnirostris* on Islas Floreana and San Cristóbal. Points 1 and 2 identify specimens that have been labelled as '*conjunctus*' and '*aureus*' respectively and considered hybrids of *Camarhynchus parvulus* and *Certhidea olivacea*; point 3 identifies a specimen referred to as '*giffordi*' and thought to be a hybrid of *Cactospiza pallida* and *Certhidea olivacea* (Lack, 1945; Bowman, 1961). Their intermediate positions on the first two Principal Component axes are consistent with these interpretations. See Table 1 for explanation of abbreviations.

The areas enclosed in the polyhedra in these Figures give an approximate measure of the degree to which populations of a species have become morphologically differentiated on different islands. Among the ground finches *G. difficilis* (six populations) is more differentiated than all others. Among the tree finches *Certhidea olivacea* (14 populations) is perhaps the most differentiated species, followed closely by *Camarhynchus psittacula* (five populations) which is clearly more differentiated than its congener *C. parvulus*, represented by the same number of populations (five). *Platyspiza crassirostris* has scarcely differentiated at all.

Geographical variation in size

In the archipelago

Geographical variation in size takes three forms in the archipelago: along altitudinal gradients, between localities at the same altitude on the same island, and between islands. Variation along altitudinal gradients cannot be examined with museum specimens because so few have altitude data recorded on the labels. It is strongly suspected to occur, but not demonstrated, from our measurements of live individuals of *G. fortis* on the south side of Is Santa Cruz, on Is Pinta and on Volcan Alcedo on Is Isabela (S. J. Millington, pers. comm.; D. S. pers. obs.). Character means were larger at higher elevations than lower ones in each case.

Lack (1945, 1947) commented on the smaller size of *G. fortis* from the northern part of Is Isabela than from the southern part of the island, and treated the samples of this species (and others) separately. We have confirmed through ANOVAS that there is small but statistically significant ($P \ll 0.05$) geographical variation in wing, tarsus and bill traits of *G. fortis* on this island. Boag (1981) has demonstrated parallel variation in this species on Is Santa Cruz with measurements of live birds.

The major source of geographical variation among populations of all species is between islands. Here we examine the possibility of systematic trends. We use a multiple linear regression analysis that employs a forward selection of variables to investigate statistical associations between population mean dimensions, estimated from male samples of 10 or more individuals, and 10 environmental variables that are correlated among themselves to varying degrees (see Abbott *et al.*, 1977): island area, elevation, number of plant species, number of other *Geospiza* species, mean latitude and mean longitude of each island, and four measures of isolation; arithmetic average of distances to all other islands ($I\ 1$), distance to nearest island ($I\ 2$), distance to nearest large island ($I\ 3$) and distance to the central large island Is Santa Cruz ($I\ 4$) (see Fig. 1). Only *Geospiza* species are considered. *G. conirostris* has too few populations to be included. Forty analyses were performed; eight dimensions (hallux not included) for five species.

Statistical associations were found in only 17 analyses (Table 10). Variation in population means of *G. scandens* is not correlated with any of the chosen variables, and only one correlation is shown by *G. fortis*. Of the remainder, some of the correlations shown by *G. magnirostris* and *G. difficilis* would probably disappear if the extinct populations on Is Santa María and San Cristóbal were included. For example, Table 10 shows that size increases in *G. magnirostris* with

Table 10. Results of multiple linear regression analyses of population means on ten environmental variables. Cumulative R^2 values are shown in parentheses. See text for explanation of the different isolation indices

	G. magnirostris	G. fortis	G. fuliginosa	G. difficilis	G. scandens
Wing	− Elevation (0.5141)		− Latitude (0.4788)		
Upper bill length			− *Geospiza* spp. (0.3319)	Longitude (0.9189)	
Lower bill length	− Area (0.5440)		− *Geospiza* spp. (0.3589)	Longitude (0.9124)	
Upper bill depth	− Longitude (0.6909)		− Latitude (0.5359)	− Isolation 2 (0.7644) Longitude (0.9485)	
Lower bill depth			− *Geospiza* spp. (0.4561) − Isolation 1 (0.6097)		
Upper bill width			− Latitude (0.4446)		
Lower bill width	− Longitude (0.5167)		− *Geospiza* spp. (0.3659) − Isolation 4 (0.5983)		
Tarsus	Latitude (0.8563)	− Latitude (0.3076)	Latitude (0.6313)		
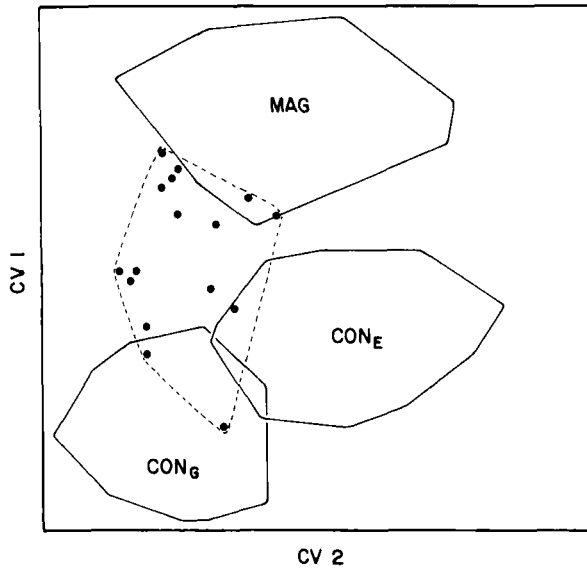
Figure 8. Canonical variates plot of eight populations of *G. magnirostris* (MAG), and, shown separately, populations of *G. conirostris* on Is Española (CON$_E$) and Is Genovesa (CON$_G$). Points refer to individuals (*darwini*) from Is Darwin. All specimens used in the analysis are males. CV1 represents a size factor, increasing away from the origin, and CV2 represents a shape factor, with the bill becoming blunter (deeper, but relatively shorter), away from the origin. The analysis was performed without the *darwini* specimens: these were projected onto the axes calculated from the remaining individuals.

decreasing elevation (wing), decreasing area (bill length), towards the east (bill depth and width) and towards the north (tarsus). Inclusion of the especially large birds from the two southeastern islands would reinforce the longitudinal trend but weaken or eliminate the rest. Only *G. fuliginosa* shows strong and consistent trends: size is greatest in the south and on poorly isolated, species-rich islands.

The consistency in *G. fuliginosa* trends is partly the product of positive character correlations. Therefore as a second exercise we use PC1 as the sole index of body size, and test for significant correlations with a reduced set of environmental variables: island area, elevation, number of plant species, mean latitude, mean longitude, and mean distance from other islands. Four tree finch species were added to the set of five ground finch species: *Platyspiza crassirostris*, *Camarhynchus psittacula*, *C. parvulus* and *Certhidea olivacea*.

Only four correlations (r) were significant. Body size was correlated positively with degree of isolation for *Certhidea olivacea* ($P < 0.01$) and *Camarhynchus parvulus* ($P < 0.05$), positively with number of plant species for *G. fortis* ($P < 0.05$), and negatively with latitude for *G. fuliginosa* ($P < 0.01$). Six analyses were performed for each of nine species, therefore two of the 54 correlations are expected to be significant at the 5 per cent level by chance alone. We attach greatest importance to the results of *G. fuliginosa* and *Certhidea olivacea* because of the significance level ($P < 0.01$).

The overall results confirm Lack's (1947) conclusion that, in contrast to many mainland species of birds, Darwin's finches do not vary morphologically in a regular geographical manner.

On small islands

Lack (1945, 1947) drew attention to the unusually small size of *G. fortis* on Is Daphne Major and the large size of *G. fuliginosa* on Los Hermanos (Crossmans). Our measurements of both museum and live specimens (Boag & Grant, 1984a; Schluter *et al.*, 1985) confirm this. The islands are very small (< 40 ha). Compared with the conspecific samples from the respective neighbouring islands of Is Santa Cruz and Is Isabela, Daphne *G. fortis* are significantly smaller ($P \ll 0.05$) in all dimensions (males and females analysed separately), while Hermanos *G. fuliginosa* (males) are significantly larger in wing length, upper bill length and lower bill width. Comparisons of unpublished measurements of live birds on Daphne Major, B. Borrero on the north shore of Santa Cruz, Hermanos and Cerro Ballena on the east shore of Isabela have confirmed these differences (see Boag & Grant, 1984a).

Two other populations on small islands are clearly different from relatives on adjacent large islands. On Is Tortuga, as on Hermanos, *G. fuliginosa* is significantly larger in beak length and width. On Is Gardner, *G. conirostris* is significantly smaller in beak length and width, and in tarsus length, than on nearby Is Española.

Samples from other small islands are very small ($N \leqslant 8$). There are significant differences between small islands and nearby large island means of one or two dimensions involving *G. fuliginosa* on Is Enderby, Is Cowley, Is Gardner by Floreana and Is Caldwell, and *G. scandens* on Is Champion and Is Gardner by Floreana. These differences may not be biologically meaningful, because some or all of the birds on the small islands may be immatures which had immigrated from the large islands. This is a probably correct explanation for the particularly small size of *G. fortis* on Is Cowley: all dimensions are significantly smaller than on nearby Is Isabela. The birds were collected on Is Cowley outside the breeding season in 1906. The next visit to Is Cowley was made in the breeding season of 1978, and only *G. fuliginosa* was observed (P. T. Boag, pers. comm.). Therefore *G. fortis* may have never been a breeding species on the island. Likewise *G. scandens* may not have bred on Is Gardner by Floreana, or else it may have become extinct, because in August 1979 one of us (P.R.G.) failed to find it (see also Grant & Schluter, 1984).

Despite the uncertain status of these small island populations the measurements are sufficient to show that none is as distinctive as *G. fortis* on Is Daphne Major and *G. fuliginosa* on Los Hermanos, and there is no morphological trend on small islands.

Geographical trends in population variation

We used the same multiple linear regression procedure as before, but substituted coefficients of variation for population means, to investigate statistical associations between population variation and environmental variables. Fourteen of 40 analyses yielded significant results (Table 11). The trends are for population variation to increase with increasing isolation and with number of other *Geospiza* species on the island. This result is interesting because these two factors negatively covary. Variation also increase from north to south in two cases, but in the opposite direction in another; and variation increases

Table 11. Results of multiple linear regression analyses of population coefficients of variation on ten environmental variables. Cumulative R^2 values are shown in parentheses. See text for explanation of the different measures of isolation

	G. magnirostris	G. fortis	G. fuliginosa	G. difficilis	G. scandens
Wing	*Geospiza* spp. (0.7058)	Isolation 2 (0.4118) *Geospiza* spp. (0.6869) − Plant spp. (0.8094) − Latitude (0.8948)			
Upper bill length		Isolation 2 (0.4245)	*Geospiza* spp. (0.2811)	Longitude (0.8017)	
Upper bill depth		Isolation 2 (0.3597)	Latitude (0.2778)		− Latitude (0.3758) Longitude (0.7754) Isolation (0.9113)
Lower bill depth		Isolation 2 (0.4921)			
Upper bill width		Isolation 4 (0.4168)	*Geospiza* spp. (0.2665)		
Lower bill width		Isolation 2 (0.6402) *Geospiza* spp. (0.8091)			
Tarsus		Isolation 4 (0.5959)	Longitude (0.2765)		

from east to west in three cases. Where correlations were strongest in *G. fuliginosa* in a geographical analysis of means, they are strongest in *G. fortis* in this analysis of variation. *G. fortis* is generally the most varying species (Table 5).

Stresemann (1936) hypothesized that poorly isolated populations of Darwin's finches exchange genes more frequently than well isolated populations and at a rate that retards, but does not prevent, differentiation. As a result, well isolated populations are more differentiated but less variable than less isolated ones. Lack (1945, 1947) and Hamilton & Rubinoff (1967) have assembled evidence in support of differentiation being a function of isolation, but the relationship with variation has not been examined before. Stresemann's hypothesis is not supported by the positive correlations between coefficients of variation and degree of isolation in Table 11.

A more direct test of the hypothesized inverse relationship is performed by first constructing an index of overall variation for a population, for example by summing coefficients of variation for all traits (Van Valen, 1974), and then correlating this with some measure of differentiation of the population. A multivariate index of differentiation can be obtained from the Mahalanobis D^2 distance of each population from the group mean. We restrict attention to the bill dimensions, as did Grant (1979) in a comparable analysis of *Fringilla coelebs* (chaffinch) populations on eight islands in the Azores.

The expected significant inverse relationship was not observed for any of the five *Geospiza* species. Non-significant negative correlation coefficients were obtained for *G. magnirostris* ($r = -0.57$; $P > 0.1$), *G. difficilis* ($r = -0.56$; $P > 0.1$) and *G. fortis* ($r = -0.08$; $P > 0.1$). But the correlation for *G. fuliginosa* was positive and significant ($r = 0.63$; $P < 0.01$). This analysis was performed a second time following deletion of two outliers, the smallest (Marchena) and largest (Hermanos) populations which are much more differentiated than the rest. The correlation for the remaining 13 populations was still significant ($r = 0.57$; $P < 0.05$). Therefore the results of this more direct test do not support Stresemann's hypothesis, and are inconsistent with the pattern exhibited by Atlantic island chaffinches (Grant, 1979). They are not without parallels, however. Power (1983) found the least two differentiated populations of *Carpodacus mexicanus* (house finch) on Californian islands to have the lowest coefficients of variation.

Since overall bill variation was also found to be a positive function of island elevation in the *Fringilla* study (Grant, 1979), we repeated the multiple linear regression analyses with the variation index as the dependent variable. The only significant result was a positive association between variation in *G. scandens* populations and the number of other *Geospiza* species on the island ($R^2 = 0.6751$); none of the correlations with island elevation approached significance. In a final set of analyses we used the differentiation index as the dependent variable, and again obtained only one significant result. The differentiation of *G. magnirostris* populations increased with distance from Is Santa Cruz ($R^2 = 0.8599$); in simple correlation analyses it increased significantly with three of the four isolation indices. Although this is the only statistically significant association in support of the arguments of Stresemann, Lack and Hamilton and Rubinoff, there is a trend in all species; all correlation coefficients for differentiation and the four measures of isolation were positive in

G. fortis, *G. fuliginosa* and *G. difficilis*, and in the case of *G. scandens* two were positive and two were negative.

<div align="center">DISCUSSION</div>

Several of our results have substantiated Lack's (1945, 1947) conclusions concerning morphological variation among populations of the same species and between different species. These results have been obtained by using data and techniques not available to Lack: weights measured in the field, and multivariate analyses and statistical procedures facilitated by a computer. Thus we have been able to show that (1) populations of the same species differ largely in size, (2) species differ conspicuously from each other in shape, especially bill shape, as well as in size in most instances, (3) the most differentiated species, i.e. those showing the most variation among populations, are *G. difficilis* and *Certhidea olivacea*, and the least differentiated species is *Platyspiza crassirostris*, (4) size variation among populations of the same species is generally not related systematically to latitude or longitude; *G. scandens* provides a good example of the typically mosaic pattern of variation in the archipelago, and (5) the populations of *G. fortis* on Is Daphne Major and *G. fuliginosa* on Is Los Hermanos are, among small island populations, the most distinctive.

The quantitative description of size and shape is not only more comprehensive, it has been extended in three areas. First, the allometric relations between dimensions among populations of the same species have been demonstrated by bivariate analysis. This has shown that wing and tarsus length covary in a very similar manner among all *Geospiza* species, whereas the relationship between bill length and bill width (or depth) differs markedly among these species. Second, it has been shown that tree finches are characterized by relatively long tarsi. Some of these species also have a relatively long hallux, as do those ground finches that spend much time either climbing on cacti or scratching on the ground. The close association between form and habit makes an adaptive explanation plausible. Parallel findings with Australian species of birds have been reported by Keast (1968).

Third, it has been shown that a tree finch species and a ground finch species overlap in principal component plots (two cases) whereas no two species within each group overlap. This result lies between two extreme alternatives; that the tree finch species and the ground finch species are entirely separable morphologically, and that each species in one group is the exact morphological counterpart of a species in the other group, only differing from it in plumage and habits. Thus there is some degree of morphological complementarity between the species of the two groups, but it is not exact.

Interpretation of these morphological patterns requires ecological study of food supply and feeding habits of the finches on each of the islands. The general paucity of strong geographical trends in our analyses can be explained by the absence from them of critical ecological data. For example it has been shown that inter-island variation in mean sizes of bill traits in *Geospiza* species is governed by inter-island variation in food supply, modified to some extent by the presence or absence of congeneric competitors (Abbott *et al.*, 1977; Smith *et al.*, 1978; Grant & Grant, 1982; Schluter & Grant, 1982; Boag & Grant, 1984a; Grant, 1984; Grant & Schluter, 1984; Schluter & Grant, 1984a; Schluter *et al.*, 1985). Therefore bill and body size variation show few simple geographical trends

probably because the pertinent characteristics of the food supply do not vary geographically in a simple way (Abbott *et al.*, 1977).

Population variation also is influenced by food supply (Bowman, 1961; Grant *et al.*, 1976; Abbott *et al.*, 1977; Grant & Price, 1981). Theoretical considerations and field studies have identified another important influence, hybridization (Grant & Price, 1981; Boag & Grant, 1984a, b). The paucity of simple geographical trends in population variation, in contrast to the results of a study of island chaffinches (Grant, 1979), can be explained in part by the fact that our analysis did not directly account for this factor. The likelihood of hybridization entered the analysis only in a highly indirect form as the number of other *Geospiza* species on an island. This is unsatisfactory because the probability of hybridization depends on which particular species coexist, as well as on how many, and which particular non-resident species immigrate (Grant & Price, 1981; Ratcliffe & Grant, 1983a; Boag & Grant, 1984a, b). Despite these and other shortcomings, coefficients of variation in *G. magnirostris*, *G. fortis* and *G. fuliginosa* increased with increasing numbers of coexisting congeners (Table 11) perhaps because this reflects a hybridization frequency directly proportional to the number of sympatric congeners. Coefficients of variation are unusually high in Darwin's finch populations (Table 5), and hybridization may be the most important responsible factor (Grant & Price, 1981; Boag & Grant, 1984a). Hybridization (with immigrant *G. fortis*) may be the cause of the only bimodal tendency in frequency distributions, manifested by the Los Hermanos population of *G. fuliginosa* (see also Lack, 1945, 1947).

Within each genus, species are identical in plumage (*Geospiza, Camarhynchus*) or nearly so (*Cactospiza*). They are distinguished by size, and in particular by the size and shape of the bill (Lack, 1945, 1947). Since individual specimens in museum collections are classified to species principally by their bill dimensions it may seem circular to claim that species differ from each other most in those features which we choose to be diagnostic. At the least it calls into question the reality of the species so recognized as collections of interbreeding individuals. Recent field studies have produced no evidence to disturb the classifications based on museum specimens. Males of species so classified sing different songs (Bowman, 1979, 1983; Ratcliffe & Grant, 1985), and discriminate between these songs and those of other species (Ratcliffe & Grant, 1985). Discrimination between conspecific and heterospecific models differing only in bill size has also been demonstrated experimentally (Lack, 1945, 1947; Ratcliffe & Grant, 1983a, b). Finally interbreeding between species classified by morphological (bill) criteria is very infrequent, whereas breeding within such species is extensive (Grant & Grant, 1980; Grant & Price, 1981; Boag & Grant, 1984b). Therefore the morphological classification of museum specimens of Darwin's finch species is sound.

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APPENDIX

Taxonomic problems

There is no general agreement on whether there are three genera of tree finches (Swarth, 1931; Bowman, 1961; Yang & Patton, 1981), two (Harris, 1974) or one (Lack, 1947). We have recognized three in Table 1 and the text, for reasons discussed by Bowman (1961) and by Lack (1947). Judgements on generic limits are based on a consideration of variation in all traits including plumage, and plumage assessment is beyond the scope of this paper. Note that Steadman (1982) advocates placing all 14 species in a single genus.

One other matter of naming is problematical. The first name given to a form of the sharp beaked ground finch, by Gould (1837) was *Geospiza nebulosa*. Owing to subsequent confusion concerning the identity and source island of the specimens the name *Geospiza difficilis* Sharpe came to replace *G. nebulosa*. Through thorough historical researches Sulloway (1982a, b) has been able to identify two of the missing specimens in the British Museum (a third is in the Royal Stockholm Museum), and there is little doubt that the source island is Is Floreana (Santa María). Our measurements of these three specimens show that this form is clearly related to other populations of *G. difficilis* (Fig. 6). Sulloway (1982a, b) has made a cogent argument for reinstating the name *nebulosa* in place of *difficilis*. Since *G. difficilis* has been the name used for the species in the modern treatments by Lack (1945, 1947) and Bowman (1961), as well as in all our own publications, we continue using it here while recognizing the force of Sulloway's arguments. The issue is currently being considered by the International Commission on Zoological Nomenclature.

Remaining problems concern the status of two species.

(1) *Geospiza conirostris*. Lack's (1945, 1947) taxonomic judgements have been widely accepted, except for the number of genera he recognized (Bowman, 1961). At the species level, the most difficult problem for him to resolve was the status of *G. conirostris*. This is summarized in the first footnote to his table III (Lack, 1947: 18): "*Geospiza conirostris* has obvious affinities with *G. scandens* and replaces it geographically, but it is so distinctive that it is given a separate specific name. It should perhaps be reckoned as part of the *G. scandens* superspecies, but this is not certain".

G. *conirostris* as currently recognized is known to have three breeding populations; on Is Española and its satellite Is Gardner (*G. c. conirostris*) and on Is Genovesa (*G. c. propinqua*). It has been reported on Is Pinta and Is Wolf (Curio & Kramer, 1965), but extensive field work on these islands in the last 10 years has failed to detect its presence (Schluter, 1982; Schluter & Grant, 1984a). It has also been reported on Is Darwin; for this situation, see below.

The distinctive feature of *G. conirostris* is lateral flattening of the bill, in which the species is more similar to the tree finches than are any of the other ground finch species. In particular, the base of the lower mandible of *G. conirostris* is flatter and less convex in profile than it is in all other *Geospiza* species. However, some individuals of *G. scandens* from Is Marchena resemble some individuals of *G. conirostris* from the adjacent island of Genovesa in this feature. We have not quantified it, but made our comparisons by placing museum specimens side by side. Clearly these two populations are similar, and it is conceivable that gene flow occurs between them even today (Grant & Grant, 1982).

Despite these similarities the overall size and shape of the bill in these two populations differ substantially. For example in Fig. 6 note the large distance between the polyhedra of these two species, particularly along the shape axis PC2. *G. conirostris* on Is Genovesa and *G. scandens* on Is Marchena are much more similar to conspecifics elsewhere than they are to each other. The populations of *G. conirostris* on Is Española and Is Gardner are slightly closer, in Fig. 6, to *G. magnirostris* and *G. fortis*. On the only island (Genovesa) where *G. conirostris* is sympatric with one of those congeners (*G. magnirostris*), interbreeding is extremely infrequent (Grant & Grant, 1982). For these reasons we continue to consider *G. conirostris* as a distinctive species.

(2) *Geospiza conirostris darwini*. An extension of the above problem is the status of the 34 specimens of large finches on Is Darwin (Culpepper), all collected within 10 years of each other at the turn of the century. Despite their exceptional variability, Lack (1947: 26) concluded: "...they all belong to *darwini*. The beak of *darwini* shows clear basic affinities with that of other forms of *G. conirostris*, but is heavier with superficial similarities to that of *G. magnirostris*". The resemblance to *G. magnirostris*, he explained, "is probably due to parallel evolution, as it is the type of beak which would be expected in a form of *G. conirostris* which had become specialized primarily for ground feeding" (p. 68). In assigning all specimens to *G. conirostris darwini*, Lack (1947) followed Rothschild & Hartert (1899, 1902).

Bowman (1961: 269), in contrast, upheld the view of Swarth (1931) that the Is Darwin birds belong to two species, *G. magnirostris* and *G. conirostris propinqua* (from Is Genovesa). Bowman (1961) corrected an error in Lack's calculations and showed that the coefficient of variation in bill depth of males ($N = 16$) was 13.13, an extremely large value.

To help resolve the issue we performed a multiple discriminant function analysis of male samples of all *G. magnirostris* populations ($N = 8$) and *G. conirostris* populations ($N = 3$), excluding the sample of males from Is Darwin. Figure 8 shows the results on the first two canonical variates axes. The 16 males from Is Darwin are projected on to the axes.

Several important points can be seen. First, there is relatively little differentiation among the *G. magnirostris* populations, hence a single composite

polyhedron is shown for the species. In contrast, the samples of *G. conirostris* from Is Genovesa and Is Española are almost entirely separated from each other; the Is Gardner sample is not shown because it is almost identical to the Is Española sample. Second, most specimens from Is Darwin do not fall into the polyhedrons of either species. Most fall in the space between *G. magnirostris* and *G. conirostris* from Is Genovesa. Third, there appears to be a bimodality in CV1 scores among the Is Darwin specimens, i.e. on the first (size) axis, eight specimens are closely allied to the *G. magnirostris* distribution and eight are closer to the *G. conirostris* (Genovesa) distribution. This reflects the two size classes perceived by Swarth (1931). The analysis provides a quantification of the taxonomic problem without indicating a solution.

We also examined the curvature of the sides of the bills (tomia) and the lateral base of the lower mandibles, as in the analysis of affinities between *G. conirostris* and *G. scandens*. In this unquantified feature, the bills of all of the Is Darwin specimens had the convex curvature of most members of the genus *Geospiza*, and not the flatter aspect of the bills of *G. conirostris*. On this basis and from the results of the discriminant function analysis we conclude that *G. conirostris*, as a species, is not represented by any of the specimens in museum collections.

The species on Is Darwin is either an unusual form of *G. magnirostris* or it deserves to be recognized as distinctive, *G. darwini* following Rothschild & Hartert (1899). The extreme variation in bill dimensions, tending towards bimodality, suggests genetic heterogeneity due to mixing. Either the species has interbred with *G. difficilis*, the only sympatric congener on the island, or else with an immigrant species: if the immigrant species was *G. conirostris*, the distinctive bill feature of that species was lost in subsequent generations. Whatever the origin of the heterogeneity it is unique among Darwin's finches.

Lack (1947) considered the possibility of a hybrid origin of the species but thought it was improbable because he had no evidence of interbreeding between *G. magnirostris* and *G. conirostris* on Is Genovesa: evidence has been obtained since then (Grant & Grant, 1982). Nevertheless recent evidence obtained elsewhere from the archipelago makes an interbreeding hypothesis plausible. On Is Daphne Major interbreeding occurs occasionally between *G. fortis* and immigrant *G. fuliginosa* and resident *G. scandens* (Grant & Price, 1981; Boag & Grant, 1984a, b). Interbreeding has the potential of elevating phenotypic and genetic variances (Grant & Price, 1981), given the high heritabilities of the major metric traits (Boag & Grant, 1978; Boag, 1983; Grant, 1983).

The finches on Is Darwin would clearly repay further study, yet the physical difficulties are formidable as the slopes of the island are too steep to be climbed. The only visit to the top of the island was made by helicopter in 1964, and in one afternoon no large finches were seen (R. I. Bowman, pers. comm.). However, on a visit in 1980 by sea to the rocky slope where the specimens had been collected earlier, one of us (D.S.) saw two individuals. One was captured and had a deep bill like that of a typical *G. magnirostris*. The other was not captured but was seen to have a longer and more pointed bill.

We conclude that the population is *G. magnirostris*, but strongly influenced by genes ultimately of heterospecific origin. We have listed it as *G. magnirostris*, in the Appendix tables, and have included it in only the bivariate analyses in Figs 3 & 4.

(3) *Geospiza magnirostris.* Five males and three females were collected on Islas Floreana and San Cristóbal by members of the Beagle expedition in 1835. In the present study we measured all but the two specimens collected by S. Covington on Is Floreana and now in the British Museum of Natural History. The two unmeasured specimens resemble the others in wing length, bill length and bill depth (Sulloway, 1982a). The combined samples from the two islands (Appendix Tables A1–A5) have larger mean wing and tarsus lengths than other populations (Fig. 3). From the relationships between wing and tarsus length on the one hand and weight on the other (Fig. 2) we estimate the weights of these birds to have been about 45 g on average, perhaps extending maximally beyond 50 g. They were thus the largest and heaviest of all Darwin's finches.

They are more distinctive in beak size (Fig. 4). They clearly differ from conspecific populations along PC2, a beak size and shape axis, but not on PC1, a body size axis (Fig. 7). The degree to which they differ from other *G. magnirostris* populations in bill dimensions is striking (Fig. 4), and is much more pronounced than is the distinctiveness of the problematical population on Is Darwin.

The question arises as to whether the populations on Islas Floreana and San Cristóbal really were conspecific with other *G. magnirostris* populations or whether they constituted a separate species. If the latter is correct they would retain the name *magnirostris*, and all other populations treated as *magnirostris* should be called *G. strenua*, the name given by Gould (1837). Swarth (1931), impressed by the confusion over their island(s) of origin, considered the specimens to be particularly large individuals from Is San Salvador, and Lack (1945) followed Swarth's taxonomic judgement. But the confusion over their origin has been removed by the historical researches of Sulloway (1982a); and all individuals are exceptionally large.

There is an interesting possibility that on San Cristóbal, at least, the large and typical forms of *G. magnirostris* were present together. One, and possibly three, specimens of the large form (*magnirostris*) were collected on this island (Sulloway, 1982a). Also collected on this island was at least one specimen of *strenua* (*sensu* Gould), by Fitzroy, and possibly two or three were collected by Darwin. Sulloway (1982a) has argued that one of Darwin's specimens was an unusually large *G. fortis*; that the other two were too small to be part of the species represented by the large form (*magnirostris*), and were therefore probably collected on another island (San Salvador); and that Fitzroy's specimen was probably a hybrid between *G. fortis* and the large form of *G. magnirostris*. If the island of origin has been correctly identified as San Cristóbal, however, the totals are one to three specimens of *magnirostris* and three or four specimens of *strenua*. They may have been sympatric species.

Since the populations on Is Floreana and Is San Cristóbal are now extinct we will never have a firm answer to the question of their taxonomic status. Fossils may shed light on the problem by showing, for example, that along one or more dimensions there is a peak between the frequency distributions of measurements that are obviously assignable to *G. fortis* and *G. magnirostris*. In view of all these uncertainties we have taken the conservative view here that the unusually large finches on these two islands are conspecific with *G. magnirostris* elsewhere in the archipelago.

Table A1. Sample size (N), mean ($\bar{x}$) and standard deviation (s.d.) for wing length (mm) of *Geospiza* species. The samples of *G. magnirostris* from Islas Floreana and San Cristóbal have been combined under the heading Floreana in this and subsequent tables: see the Appendix text for a discussion of the taxonomic status of these populations and the population of *G. magnirostris* on Is Darwin

	♂♂			♀♀		
	N	$\bar{x}$	s.d.	N	$\bar{x}$	s.d.
G. magnirostris						
Santa Cruz	27	82.3	2.74	16	78.6	2.00
San Salvador	57	83.4	2.69	37	80.6	2.56
Rábida	40	83.3	2.72	17	80.4	2.62
Isabela	7	80.9	3.24	8	79.9	3.48
Genovesa	38	86.5	2.56	23	82.8	2.21
Marchena	53	81.9	3.06	19	78.3	2.66
Pinta	62	82.6	2.57	36	80.7	2.16
Wolf	8	87.2	2.31	4	84.2	1.71
Darwin	16	84.4	3.28	8	80.1	3.60
Floreana	4	89.0	1.41	2	87.0	—
G. fortis						
Española	4	70.7	0.96	7	70.0	1.91
Floreana	278	72.8	2.73	229	69.7	2.33
Gardner/Floreana	4	73.7	2.87	5	70.8	3.70
Champion	4	73.0	2.94	—	—	—
San Cristóbal	134	73.1	3.24	87	70.9	2.68
Santa Fe	9	74.9	2.57	4	68.2	4.03
Santa Cruz	159	72.8	3.23	110	70.5	3.16
Baltra	25	72.6	2.63	30	69.3	2.68
Daphne	31	68.6	1.78	11	65.9	1.81
San Salvador	86	71.9	2.22	57	69.5	2.65
Rábida	11	72.3	1.74	11	69.0	1.41
Pinzón	39	68.9	3.05	30	68.6	2.53
Cowley	5	70.4	2.07	—	—	—
Isabela	198	73.2	3.39	127	70.8	3.12
Fernandina	14	71.6	1.86	3	70.0	2.00
Marchena	44	67.4	1.47	25	64.6	1.35
Pinta	59	66.0	2.24	28	63.3	1.84
G. fuliginosa						
Española	37	64.7	1.82	20	62.3	2.13
Gardner/Española	12	64.2	2.52	6	61.8	1.17
Floreana	97	64.0	1.99	101	62.1	1.51
Gardner/Floreana	8	65.4	2.50	4	62.2	1.50
Caldwell	3	65.0	2.65	—	—	—
Enderby	8	64.7	1.39	7	61.3	2.50
San Cristóbal	150	64.2	1.82	126	62.1	1.73
Santa Fe	50	63.7	1.71	12	61.4	1.88
Santa Cruz	134	64.0	1.62	70	61.5	1.77
Baltra	47	64.3	1.63	28	61.6	1.39
Bartolomé	5	63.4	2.19	—	—	—
San Salvador	39	63.8	2.12	24	62.2	2.06
Rábida	14	64.0	1.57	12	61.8	1.85
Pinzón	98	64.1	1.74	32	61.8	1.62
Cowley	4	63.5	2.65	4	62.0	1.41
Hermanos	12	66.5	1.79	5	63.2	2.59
Tortuga	11	64.7	1.49	7	62.6	0.53
Isabela	202	64.5	1.78	149	61.7	1.68
Fernandina	27	64.8	1.87	17	62.7	1.86
Marchena	39	59.2	2.09	30	57.1	1.92
Pinta	63	59.8	1.78	43	58.7	1.87

Table A1. Continued

	♂♂			♀♀		
	N	x̄	S.D.	N	x̄	S.D.
G. difficilis						
Floreana	1	72	—	2	71.5	—
Santa Cruz	31	70.3	1.30	10	68.7	1.10
San Salvador	52	73.0	1.80	25	70.8	1.44
Genovesa	83	63.4	2.02	44	61.3	1.68
Pinta	19	63.4	1.39	15	62.5	1.30
Wolf	100	72.9	1.84	49	70.1	1.61
Darwin	39	74.4	2.03	9	71.3	1.58
G. scandens						
Floreana	141	71.6	1.97	92	69.3	1.76
Gardner/Floreana	4	71.0	1.15	—	—	—
Champion	4	72.5	1.29	6	68.5	1.76
San Cristóbal	6	69.5	2.59	10	67.6	2.17
Santa Fe	66	72.4	1.76	28	70.0	1.89
Santa Cruz	127	72.8	2.09	76	70.4	2.08
Baltra	50	72.8	2.05	29	70.0	1.52
San Salvador	29	70.7	1.64	17	67.6	1.66
Rábida	23	71.8	2.33	13	68.8	1.40
Pinzón	8	72.0	1.07	12	70.6	2.23
Isabela	23	72.8	1.76	9	69.9	2.52
Marchena	10	73.5	2.27	13	70.5	1.85
Pinta	16	72.5	1.75	13	69.1	2.30
G. conirostris						
Española	120	80.3	2.58	77	76.9	2.00
Gardner/Española	76	79.5	2.61	50	76.4	2.18
Genovesa	65	77.7	2.17	34	74.4	2.15

Table A2. Sample size (N), mean (x̄) and standard deviation (S.D.) for tarsus length (mm) of each *Geospiza* species

	♂♂			♀♀		
	N	x̄	S.D.	N	x̄	S.D.
G. magnirostris						
Santa Cruz	27	21.03	0.96	16	20.23	0.80
San Salvador	57	20.98	1.01	37	20.80	0.98
Rábida	40	20.71	0.63	17	20.51	0.57
Isabela	7	20.53	1.23	8	20.49	1.15
Genovesa	38	21.45	0.88	22	21.12	1.15
Marchena	54	21.04	0.80	20	20.79	1.07
Pinta	62	21.36	0.76	36	20.39	0.94
Wolf	8	22.22	1.35	4	20.60	1.56
Darwin	16	21.92	0.70	8	21.36	0.84
Floreana	4	22.18	0.63	2	21.25	—
G. fortis						
Española	4	18.75	0.83	7	18.26	0.89
Floreana	278	18.81	0.84	228	18.23	0.69
Gardner/Floreana	4	18.72	1.47	5	18.36	0.74
Champion	4	18.77	1.21	—	—	—
San Cristóbal	134	19.12	0.84	87	18.69	0.76
Santa Fe	9	19.06	0.64	4	18.22	0.66
Santa Cruz	160	18.82	0.87	110	18.16	0.76
Baltra	25	18.76	0.76	30	18.04	0.79
Daphne	31	17.75	0.81	11	17.01	0.73

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Table A2. Continued

	♂♂			♀♀		
	N	x̄	s.d.	N	x̄	s.d.
San Salvador	86	18.54	0.68	57	18.02	0.91
Rábida	11	19.01	0.52	11	18.11	0.70
Pinzón	39	17.94	0.94	30	17.79	0.95
Cowley	5	18.62	0.29	—	—	—
Isabela	197	19.03	1.04	127	18.59	0.82
Fernandina	14	18.30	0.70	3	17.40	1.04
Marchena	44	17.23	0.85	25	16.86	0.74
Pinta	58	17.20	0.73	28	16.45	0.55
G. fuliginosa						
Española	37	17.12	0.71	20	16.49	0.78
Gardner/Española	12	17.24	0.78	6	16.40	0.54
Floreana	97	17.19	0.57	101	16.69	0.63
Gardner/Floreana	8	17.21	0.55	4	16.65	0.40
Caldwell	3	16.30	0.61	—	—	—
Enderby	8	16.44	0.47	7	15.84	0.24
San Cristóbal	148	17.13	0.66	125	16.66	0.77
Santa Fe	50	16.77	0.68	12	16.43	0.82
Santa Cruz	132	16.97	0.57	70	16.50	0.53
Baltra	46	16.88	0.56	27	16.47	0.64
Bartolomé	5	17.02	0.38	—	—	—
San Salvador	39	17.08	0.62	24	16.73	0.66
Rábida	14	17.03	0.75	12	16.30	0.74
Pinzón	98	16.99	0.65	32	16.47	0.47
Cowley	4	17.32	0.61	4	17.22	0.74
Hermanos	12	17.22	0.74	5	16.78	0.85
Tortuga	11	16.77	0.53	7	16.60	0.54
Isabela	201	17.06	0.56	149	16.65	0.69
Fernandina	27	16.85	0.82	17	16.64	0.61
Marchena	38	15.53	0.49	30	15.14	0.72
Pinta	62	15.71	0.75	41	15.39	0.66
G. difficilis						
Floreana	1	18.9	—	2	20.7	—
Santa Cruz	31	18.61	0.94	10	18.90	0.80
San Salvador	52	19.66	0.98	25	19.09	1.21
Genovesa	83	16.37	0.74	44	15.91	0.64
Pinta	19	17.17	1.11	15	17.12	0.99
Wolf	100	18.77	0.58	49	18.03	0.67
Darwin	39	19.26	0.72	10	18.71	0.81
G. scandens						
Floreana	141	18.80	0.76	92	18.29	0.64
Gardner/Floreana	4	18.60	0.53	—	—	—
Champion	4	17.50	1.19	6	18.23	0.61
San Cristóbal	6	17.98	1.07	10	17.78	0.87
Santa Fe	66	19.13	0.78	28	18.42	0.62
Santa Cruz	126	19.11	0.67	76	18.74	0.70
Baltra	50	19.17	0.49	29	18.48	0.60
San Salvador	29	18.33	1.03	17	18.01	0.90
Rábida	23	18.70	0.71	13	17.85	0.71
Pinzón	8	18.99	0.51	12	18.49	1.00
Isabela	23	19.06	0.66	9	18.67	0.71
Marchena	9	19.34	0.81	13	18.57	0.97
Pinta	16	19.28	0.39	13	18.50	0.53
G. conirostris						
Española	120	20.06	0.75	76	19.43	0.64
Gardner/Española	76	19.61	0.81	50	19.20	0.94
Genovesa	65	20.67	0.80	34	20.02	0.78

Table A3. Sample size (N), mean ($\bar{x}$) and standard deviation (s.d.) for upper mandible length (mm) of each *Geospiza* species

	♂♂			♀♀		
	N	$\bar{x}$	s.d.	N	$\bar{x}$	s.d.
G. magnirostris						
Santa Cruz	27	14.94	0.82	16	14.63	0.70
San Salvador	57	15.55	1.21	37	15.01	1.14
Rábida	40	15.11	0.75	17	14.73	0.80
Isabela	7	14.67	1.25	8	14.18	1.24
Genovesa	38	16.07	1.00	23	15.81	0.78
Marchena	54	14.96	0.72	20	14.73	0.98
Pinta	62	15.78	0.75	36	15.41	0.66
Wolf	8	15.36	0.59	4	15.92	0.29
Darwin	16	14.69	1.07	8	14.79	1.19
Floreana	4	17.98	0.71	2	17.35	—
G. fortis						
Española	4	10.95	0.40	7	11.27	0.78
Floreana	278	11.26	0.90	227	10.91	0.80
Gardner/Floreana	4	11.55	1.13	5	11.10	1.23
Champion	4	11.40	1.00	—	—	—
San Cristóbal	134	11.96	0.75	87	11.75	0.78
Santa Fe	9	12.30	1.22	4	10.92	0.50
Santa Cruz	159	11.66	0.87	110	11.46	0.75
Baltra	25	11.22	0.69	30	11.14	0.65
Daphne	31	10.26	0.58	11	10.08	0.77
San Salvador	85	11.16	0.63	56	11.01	0.83
Rábida	11	11.27	0.47	11	11.04	0.61
Pinzón	39	10.68	0.78	30	10.85	0.86
Cowley	5	10.70	0.41	—	—	—
Isabela	198	11.55	1.03	126	11.29	0.95
Fernandina	14	11.24	0.38	3	11.13	0.65
Marchena	44	11.36	0.53	25	11.16	0.47
Pinta	59	10.93	0.61	28	10.76	0.57
G. fuliginosa						
Española	37	8.39	0.33	20	8.25	0.43
Gardner/Española	12	8.30	0.49	6	8.03	0.51
Floreana	97	8.33	0.40	101	8.13	0.51
Gardner/Floreana	8	8.66	0.49	4	8.42	0.32
Caldwell	3	8.50	0.20	—	—	—
Enderby	8	7.89	0.48	7	7.93	0.39
San Cristóbal	149	8.53	0.69	125	8.37	0.69
Santa Fe	50	8.49	0.42	11	8.06	0.22
Santa Cruz	134	8.18	0.46	70	8.08	0.49
Baltra	47	8.29	0.43	27	8.18	0.35
Bartolomé	5	8.10	0.19	—	—	—
San Salvador	38	8.14	0.38	24	8.30	0.51
Rábida	14	8.19	0.46	12	8.14	0.34
Pinzón	98	8.32	0.39	32	8.27	0.32
Cowley	3	7.97	0.70	4	7.07	0.39
Hermanos	12	9.00	0.96	5	8.84	0.81
Tortuga	11	8.59	0.40	7	8.40	0.28
Isabela	201	8.04	0.39	149	7.90	0.37
Fernandina	27	7.76	0.58	17	7.73	0.49
Marchena	38	7.78	0.34	30	7.68	0.32
Pinta	62	8.02	0.42	43	7.81	0.44
G. difficilis						
Floreana	1	10.5	—	2	10.95	· ·
Santa Cruz	31	9.25	0.33	10	9.14	0.55
San Salvador	52	9.89	0.44	25	9.72	0.36

Table A3. Continued

	♂♂			♀♀		
	N	x̄	S.D.	N	x̄	S.D.
Genovesa	83	9.06	0.50	43	8.96	0.48
Pinta	19	9.34	0.57	15	9.17	0.36
Wolf	100	10.45	0.47	49	10.36	0.44
Darwin	38	11.13	0.42	10	10.89	0.53
G. scandens						
Floreana	140	13.39	0.77	91	13.10	0.78
Gardner/Floreana	4	12.85	0.81	—	—	—
Champion	4	13.02	0.94	6	12.65	0.72
San Cristóbal	6	13.02	0.93	10	12.35	1.11
Santa Fe	66	14.08	0.78	28	13.77	0.80
Santa Cruz	125	14.53	1.02	74	14.35	0.93
Baltra	49	14.47	0.85	29	14.42	0.66
San Salvador	29	12.68	0.66	17	12.06	0.87
Rábida	23	13.15	0.62	13	13.18	1.12
Pinzón	8	14.36	0.55	12	13.79	0.95
Isabela	23	14.06	0.83	9	13.64	1.03
Marchena	10	14.90	0.57	13	14.47	0.64
Pinta	16	14.27	0.52	13	13.78	0.91
G. conirostris						
Española	119	15.03	1.08	77	14.55	0.98
Gardner/Española	76	14.36	0.97	49	13.77	0.98
Genovesa	64	14.06	0.85	33	13.69	0.59

Table A4. Sample size (N), mean (x̄) and standard deviation (S.D.) for upper mandible depth in millimetres of each *Geospiza* species

	♂♂			♀♀		
	N	x̄	S.D.	N	x̄	S.D.
G. magnirostris						
Santa Cruz	27	7.68	0.97	16	7.37	0.86
San Salvador	57	8.30	0.77	37	7.72	0.81
Rábida	40	7.65	0.49	17	7.25	0.54
Isabela	7	6.99	0.84	8	7.17	0.74
Genovesa	38	8.53	0.70	23	8.52	0.70
Marchena	54	7.85	0.66	20	7.48	0.84
Pinta	62	8.31	0.63	36	7.86	0.57
Wolf	8	7.59	0.89	4	7.90	0.50
Darwin	16	6.61	1.04	8	6.05	0.65
Floreana	4	9.45	0.37	2	9.20	
G. fortis						
Española	4	5.22	0.26	7	5.27	0.40
Floreana	278	5.29	0.57	229	5.13	0.45
Gardner/Floreana	4	5.30	1.04	5	4.92	0.08
Champion	4	5.25	0.26	—		-
San Cristóbal	134	5.60	0.60	87	5.49	0.59
Santa Fe	9	5.51	0.72	4	4.50	0.56
Santa Cruz	158	5.26	0.65	110	5.08	0.58
Baltra	25	5.27	0.46	30	4.96	0.52

Table A4. Continued

	♂♂			♀♀		
	N	x̄	s.d.	N	x̄	s.d.
Daphne	31	4.38	0.45	11	4.31	0.27
San Salvador	86	5.26	0.48	57	5.12	0.53
Rábida	11	5.17	0.47	11	5.14	0.57
Pinzón	39	4.82	0.58	30	5.03	0.60
Cowley	5	4.62	0.26	—	—	—
Isabela	198	5.37	0.74	127	5.27	0.68
Fernandina	14	5.30	0.23	3	5.23	0.38
Marchena	44	4.98	0.46	25	4.88	0.42
Pinta	59	4.80	0.45	28	4.49	0.38
G. fuliginosa						
Española	37	3.59	0.24	20	3.55	0.22
Gardner/Española	12	3.57	0.29	6	3.68	0.12
Floreana	96	3.49	0.28	101	3.48	0.22
Gardner/Floreana	8	3.55	0.45	4	3.27	0.46
Caldwell	3	3.27	0.20		—	—
Enderby	8	3.36	0.47	7	3.37	0.27
San Cristóbal	150	3.54	0.34	126	3.44	0.33
Santa Fe	50	3.47	0.27	12	3.38	0.31
Santa Cruz	135	3.38	0.32	70	3.39	0.27
Baltra	47	3.57	0.29	28	3.39	0.28
Bartolomé	5	3.22	0.37	—	—	
San Salvador	39	3.39	0.30	24	3.36	0.47
Rábida	14	3.38	0.25	12	3.17	0.37
Pinzón	98	3.46	0.26	32	3.49	0.27
Cowley	4	3.25	0.47	4	3.30	0.62
Hermanos	12	3.54	0.51	5	3.42	0.48
Tortuga	11	3.64	0.29	7	3.57	0.31
Isabela	202	3.50	0.32	149	3.43	0.30
Fernandina	27	3.42	0.41	17	3.33	0.31
Marchena	39	3.12	0.26	30	2.97	0.29
Pinta	63	3.28	0.32	43	3.19	0.29
G. difficilis						
Floreana	1	4.4	—	2	4.00	—
Santa Cruz	31	4.22	0.42	10	4.25	0.29
San Salvador	52	4.50	0.41	25	4.38	0.37
Genovesa	83	3.25	0.31	44	3.18	0.33
Pinta	19	3.75	0.42	15	3.78	0.25
Wolf	100	3.78	0.29	49	3.64	0.28
Darwin	39	4.08	0.40	10	3.99	0.34
G. scandens						
Floreana	141	4.33	0.31	92	4.21	0.30
Gardner/Floreana	4	4.37	0.27	—	—	—
Champion	4	4.02	0.51	6	3.77	0.50
San Cristóbal	6	4.25	0.41	10	4.02	0.64
Santa Fe	66	4.63	0.37	28	4.44	0.45
Santa Cruz	127	4.41	0.41	75	4.23	0.38
Baltra	50	4.47	0.35	29	4.27	0.40
San Salvador	29	3.77	0.40	17	3.81	0.35
Rábida	23	4.08	0.50	13	4.21	0.50
Pinzón	8	4.35	0.53	12	4.37	0.25
Isabela	23	4.49	0.42	9	4.21	0.31
Marchena	10	4.92	0.37	13	4.70	0.37
Pinta	16	4.52	0.33	13	4.36	0.35
G. conirostris						
Española	120	6.24	0.62	77	5.97	0.57
Gardner/Española	76	6.17	0.47	50	5.82	0.53
Genovesa	65	5.70	0.50	34	5.44	0.57

Table A5. Sample size (N), mean ($\bar{x}$) and standard deviation (s.d.) for lower mandible width (mm) of each *Geospiza* species

	♂♂			♀♀		
	N	$\bar{x}$	s.d.	N	$\bar{x}$	s.d.
G. magnirostris						
Santa Cruz	27	14.56	1.10	16	13.88	0.99
San Salvador	57	15.07	1.20	37	14.64	1.09
Rábida	40	13.73	0.67	17	13.29	0.94
Isabela	7	13.69	1.12	8	13.39	1.73
Genovesa	38	15.87	0.69	23	15.56	0.47
Marchena	54	14.32	0.85	20	13.72	1.01
Pinta	62	15.24	0.80	36	14.44	0.63
Wolf	8	14.86	0.52	4	14.35	0.29
Darwin	16	12.56	1.55	8	11.91	1.29
Floreana	4	17.43	1.09	2	16.85	....
G. fortis						
Española	4	8.87	0.29	7	9.54	0.56
Floreana	276	9.56	1.05	229	9.05	0.72
Gardner/Floreana	4	9.92	1.24	5	9.26	0.54
Champion	4	9.47	0.75	—	—	
San Cristóbal	134	10.21	0.93	87	9.80	0.91
Santa Fe	9	10.19	0.92	4	8.87	0.56
Santa Cruz	160	9.96	0.98	110	9.49	0.93
Baltra	25	9.62	0.76	29	9.17	0.73
Daphne	31	8.17	0.53	11	7.98	0.53
San Salvador	86	9.56	0.66	57	9.38	0.86
Rábida	11	9.84	0.45	11	9.24	0.49
Pinzón	39	8.73	0.93	30	8.84	1.11
Cowley	5	8.94	0.30	—	—	.
Isabela	198	9.92	1.06	127	10.11	0.90
Fernandina	14	9.36	0.34	3	9.13	0.25
Marchena	44	9.17	0.46	25	9.14	0.40
Pinta	59	9.04	0.64	28	8.58	0.42
G. fuliginosa						
Española	36	6.58	0.35	20	6.22	0.29
Gardner/Española	11	6.58	0.25	6	6.28	0.31
Floreana	97	6.54	0.31	100	6.27	0.29
Gardner/Floreana	8	6.80	0.32	4	6.17	0.25
Caldwell	3	6.60	0.17	—	—	—
Enderby	8	6.57	0.49	7	6.27	0.34
San Cristóbal	149	6.46	0.42	126	6.19	0.36
Santa Fe	49	6.55	0.36	12	6.28	0.25
Santa Cruz	135	6.48	0.29	70	6.28	0.29
Baltra	46	6.57	0.30	28	6.39	0.26
Bartolomé	5	6.60	0.23	—	—	—
San Salvador	38	6.47	0.34	24	6.34	0.48
Rábida	14	6.51	0.41	12	6.31	0.19
Pinzón	98	6.57	0.30	31	6.41	0.26
Cowley	4	6.20	0.53	4	6.05	0.17
Hermanos	12	7.18	0.59	5	7.00	0.38
Tortuga	11	6.85	0.35	7	6.59	0.21
Isabela	201	6.53	0.32	148	6.38	0.27
Fernandina	27	6.46	0.29	16	6.16	0.31
Marchena	38	5.77	0.29	30	5.61	0.38
Pinta	63	6.28	0.32	43	6.06	0.30
G. difficilis						
Floreana	1	8.0	—	2	8.85	—
Santa Cruz	31	7.18	0.30	10	7.07	0.25
San Salvador	50	7.68	0.43	24	7.39	0.26

Table A5. Continued

	♂♂			♀♀		
	N	$\bar{x}$	s.d.	N	$\bar{x}$	s.d.
Genovesa	81	6.21	0.34	44	6.00	0.37
Pinta	19	6.83	0.65	15	6.53	0.32
Wolf	100	6.87	0.36	48	6.66	0.31
Darwin	39	7.42	0.32	10	7.15	0.21
G. scandens						
Floreana	141	7.77	0.33	92	7.39	0.37
Gardner/Floreana	4	7.90	0.11	—	—	—
Champion	4	7.77	0.39	6	7.57	0.39
San Cristóbal	6	7.72	0.32	10	7.42	0.56
Santa Fe	66	8.08	0.44	28	7.68	0.32
Santa Cruz	126	7.90	0.48	76	7.62	0.40
Baltra	50	7.84	0.42	29	7.59	0.33
San Salvador	29	7.25	0.45	17	6.75	0.40
Rábida	22	7.56	0.45	13	7.41	0.52
Pinzón	8	8.14	0.33	12	7.43	0.47
Isabela	23	7.90	0.50	9	7.22	0.43
Marchena	10	8.69	0.56	13	8.40	0.54
Pinta	16	8.07	0.48	13	7.45	0.56
G. conirostris						
Española	119	11.71	0.92	77	11.00	0.76
Gardner/Española	76	11.25	0.77	50	10.74	0.82
Genovesa	65	9.79	0.74	34	9.45	0.75