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Hybridization of Darwin's finches on Isla Daphne Major, Galápagos

PETER R. GRANT

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544–1003, U.S.A.

SUMMARY

There has been much debate in the past about whether Darwin's finches hybridize in nature, and if they do whether hybridization could account for the intermediate appearance of certain forms. To resolve these issues the breeding of all finches on the small Galápagos island of Daphne Major was studied in every year from 1976 to 1992. The island supported breeding populations of *Geospiza fortis* (harmonic mean of 198 breeding individuals), *G. scandens* ($H = 80$), *G. fuliginosa* ($H = 3$) and, in the past 10 years, *G. magnirostris* ($H = 6$). Morphological criteria for defining species were developed in a study of the finches on the neighboring large island of Santa Cruz. These were then used with modification on Daphne to classify members of the first few generations to species. Observations of breeding birds showed that in a few cases species interbred.

G. fortis hybridized with *G. fuliginosa* in 11 out of the 13 years in which both species bred. *G. fortis* and *G. scandens* hybridized in six of the years. Hybridization was always rare. Hybridizing individuals constituted 1.8% of breeding *G. fortis*, on average, 0.8% of *G. scandens*, but 73.0% of the much rarer *G. fuliginosa*. F_1 hybrids were viable and fertile. They rarely bred with each other to produce an F_2 generation. Much more frequently they backcrossed to the common species, *G. fortis* and *G. scandens*. In all these cases hatching and fledging success were high, giving scarcely any indication of genetic incompatibilities in the F_1, F_2 or backcross generations.

The demonstration of natural hybridization answers some questions and raises others. It shows that introgression of genes could be a small factor contributing to the intermediate appearance of *G. fortis* on Daphne Major: that is between typically larger forms of this species elsewhere in the archipelago and the smaller *G. fuliginosa*. However hybridization with the larger *G. scandens* has the opposite directional effect on *G. fortis*. Hybridization and introgression sometimes complement the effects of natural selection, sometimes they are opposed by it. Introgression also contributes to the large morphological variation displayed by this and several other populations in the archipelago. Hybridization raises questions about how species of Darwin's finches (and other organisms) should be defined and recognized. In terms of the broad biological species concept there are four species of finches on Daphne Major, neither completely independent evolutionarily on the one hand (except for *G. magnirostris*), nor approaching panmixia on the other hand.

1. INTRODUCTION

The role of hybridization in the diversification of Darwin's Finches has been much debated. The first modern treatment of the finches (family Geospizinae; Passeriformes) was made by Lack (1945, 1947) following four months of fieldwork on the Galápagos and an exhaustive study of specimens in museum collections. He had been stimulated to undertake the field study by an address commemorating the centenary of Darwin's visit to the islands (Lowe 1936). Lowe (1930, 1936) had suggested that hybridization was the explanation for the large amount of morphological variation displayed collectively by this group of closely-related finches. Failing to find in the writings of visitors to the islands any indication of sufficient environmental heterogeneity to account for the sympatric occurrence of many species, some highly variable, he wrote (1936, pp. 320–321); 'it is difficult to resist the conclusion that in the finches of the Galápagos we are faced with a swarm of hybridization segregates which remind us strangely of the "plant" swarms described by Cockayne and Lotsey in New Zealand forests as the result of natural crossings. I think it was William Bateson who always maintained that the finches of the Galápagos could only be explained on the assumption that they were the segregates of a cross between ancestral forms distributed over a large ancestral area which was subsequently broken up by subsidencies or upthrusts leading to the present disposition of the islands'.

Lack (1945, 1947) made detailed observations of finches in the breeding season of 1938–39, yet failed to find any instance of interbreeding. Attempts to induce interbreeding among four species in captivity failed (Orr 1945). Although Lack (1945) initially attached

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importance to hybridization, he later rejected Lowe's suggestions on empirical grounds, and wrote (Lack 1947, p. 100) 'Some forms of Darwin's finches are intermediate in appearance between two species, but in most cases this is probably due to the intermediate nature of their ecological requirements and not to a hybrid origin. There are also a number of freak specimens, but it is not certain how many of these are hybrids, and their rarity indicates that they are at a disadvantage, though selection is evidently less strict than is the case in most birds. To conclude, it seems probable that hybridization has not played an important part in the origin of new forms of Darwin's finches'.

Since 1947, and prior to the study reported here, hybridization in the Galápagos has been neither neglected nor satisfactorily demonstrated. Snow (1966) suggested that hybridization could explain the large variation displayed by three species of ground finches (*Geospiza*) on the south side of Santa Cruz island, and the absence of clear distinctions between the species at this locality (see also G. L. Stebbins in Bowman (1961), and Vagvolgyi & Vagvolgyi (1990)). In the laboratory Bowman (1983) observed a mixed mating of the ground finch species *G. scandens* from Santa Cruz island and *G. difficilis* from Wolf. The eggs hatched but the offspring died two days later. On Santa Cruz island he collected a male tree finch intermediate in morphology between *Certhidea olivacea* (warbler finch) and *Camarhynchus parvulus* (small tree finch). It sang the song of each species, and may have been a hybrid. If so it was backcrossing, as it was paired with a small tree finch that had a nest with three nestlings. This single observation is significant in the light of three morphologically similar specimens in museum collections. Originally described as different species (Swarth 1931), they were identified by Stresemann (1936) as intergeneric hybrids.

Congeneric species are distinguished by their measurements and not by plumage (Lack 1945, 1947). Song features of some but not all populations are distinctive enough to identify males (Bowman 1979, 1983; Ratcliffe 1981; Grant 1984; Ratcliffe & Grant 1985), but females do not sing these songs, so for an unambiguous demonstration of interbreeding in nature neither observations or tape-recorded song are sufficient; measurements of individually recognizable birds are needed.

Thus two debated issues remain unresolved; whether hybridization occurs in nature, and if it does whether it could account for the intermediate appearance of certain forms.

The study reported here was started in 1976 on the small island of Daphne (0.34 km^2) in part to resolve these issues (Boag & Grant 1984). The island is in the centre of the archipelago and 8 km distant from the much larger island of Santa Cruz (904 km^2; figure 1). It is the most suitable location for a study of hybridization. It is uninhabited and undisturbed, and it supports a population of medium ground finches, *Geospiza fortis*, considered by Lack as one of the 'intermediate' forms. The population is intermediate between typical finches of this species elsewhere in the archipelago, and a smaller species also widely distributed in the archipelago but apparently absent from Daphne: *G. fuliginosa*, the small ground finch. The

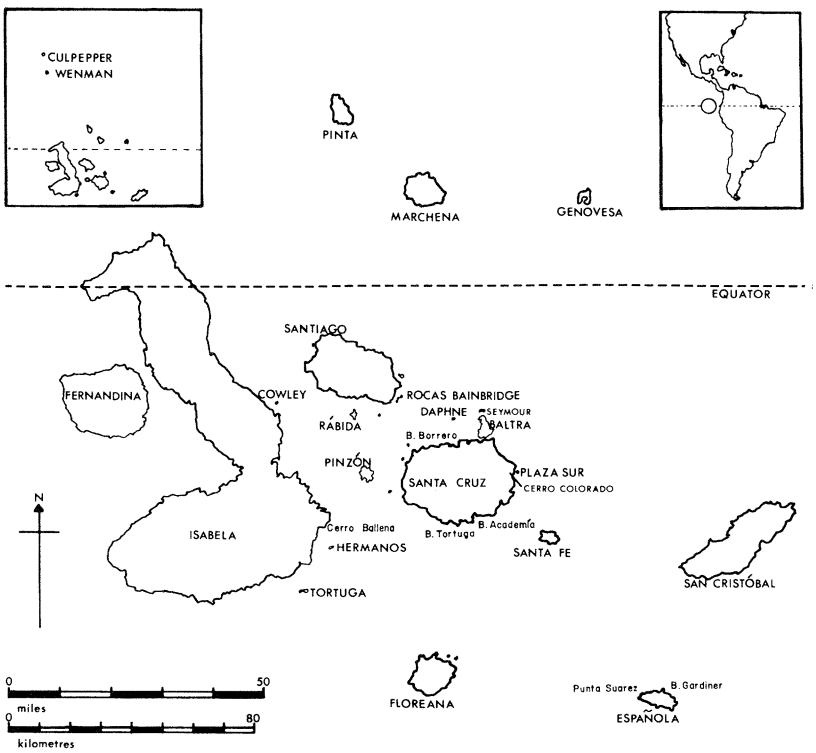

Figure 1. Map of the Galápagos islands south of the equator. Daphne is 8 km to the north of Santa Cruz (Bahía Borrero) and 8 km to the west of Baltra and Seymour. From Boag & Grant (1984).

small size of the island has made it possible to study the entire population of breeding finches.

2. METHODS

Methods have been described extensively elsewhere (Abbott *et al.* 1977; Boag & Grant 1984; Gibbs & Grant 1987*a*), and will only be summarized here. Finches have been studied on the island in every year since 1973. Adults and immatures have been captured in mist nets, measured, ringed with a unique combination of one numbered metal ring and three coloured plastic (PVC) rings coded to correspond to the numbers on the metal ring, and released. Nestlings have been ringed in a similar manner and measured upon recapture when fully grown (i.e. 60 days or older; Boag 1984). Measurements taken were weight in grams, wing length, tarsus length, and bill length, depth and width in millimetres. Most measurements were made by the author. Correction factors for the remainder were calculated from birds measured by the author and other measurers.

Repeatability of measurements made by the same or different measurers is high for all traits (e.g. Boag 1983; P. R. Grant & B. R. Grant 1993). Statistical methods of analysis are described in § 3.

The breeding of finches has been studied in every year since 1976. The reproductive fates of approximately two-thirds of all breeding finches were determined in 1976–78. In subsequent years all breeding birds have been followed and approximately 97% of all nestlings have been ringed. *G. fortis* is not the only species of finch breeding on the island. Other species are *G. scandens* (cactus finch), and the supposedly absent species *G. fuliginosa* (small ground finch; see also Harris (1973)) and *G. magnirostris* (large ground finch).

3. RESULTS

(*a*) *Classifying individuals to species*

(i) *The species of finches on Isla Santa Cruz*

As a result of morphological intermediacy, identifying individual finches on Daphne presents problems in some cases. The starting point for developing methods of identifying finches there is the adjacent island of Santa Cruz. Daphne is a small satellite of this large island (figure 1), and the finches on Daphne were almost certainly derived from populations on Santa Cruz. In a study site (Bahía Borrero) on the north coast of Santa Cruz near the closest point to Daphne, 460 ground finches were captured and measured in 1973 and 1975. Aside from a single individual of *Geospiza magnirostris* and one unidentified finch they belonged to three species: *G. fortis* (225), *G. fuliginosa* (208) and *G. scandens* (25). Most of their frequency distributions of single dimensions like beak length are contiguous or overlap very slightly (figure 2*a*), whereas on a bivariate plot of bill depth against bill length the clusters are discrete (figure 2*b*). These patterns of variation are repeated on many islands in the archipelago (Lack 1945, 1947; Grant *et al.* 1985). Measurements of the two traits define the species.

The discreteness of the clusters permits an assignment of all Santa Cruz individuals (except one) to species by inspection of the bivariate plot. *G. fuliginosa* and *G. fortis* are separated on the beak depth axis, whereas *G. scandens* and *G. fortis* differ by a combination of the two dimensions rather than by either alone. An exceptional individual identified on the plot (figure 2*b*) is impossible to assign and may be a hybrid. It is possible that some of the peripheral members of the *G. fortis* cluster are also hybrids. Nevertheless the classification can be used in a discriminant function analysis to maximally separate the groups on a synthetic axis, and to thereby identify the traits that contribute most to the separation. Boag & Grant (1984) performed this analysis with the combined sample of 182 *G. fortis* and *G. fuliginosa* measured in 1975. They confirmed what is evident from univariate analyses, namely that beak dimensions contribute most to the separation, and wing length, tarsus length, and mass contribute the least.

In fact the separations can be made simply, as follows. In the combined distribution of beak depth measurements of *G. fuliginosa* and *G. fortis* there is a gap of 0.5 mm from 8.3 to 8.7 mm. Outside this region there is no other gap of more than 0.1 mm in the combined range from 5.9 mm, the smallest *G. fuliginosa*, to 12.1 mm, almost the largest *G. fortis*. Beak depth measurements clearly distinguish the two species. Frequency distributions of the other two beak dimensions of the combined sample lack comparable gaps. The largest gap on the beak width axis is 0.2 mm and the largest on the beak length axis is 0.1 mm. Distributions of other body size – related traits also lack comparable gaps, as do all traits in the combined sample of *G. fortis* and *G. scandens*.

On a beak depth axis the largest *G. scandens* has the same measurement (8.8 mm) as the smallest *G. fortis*. However, owing to almost non-overlapping beak length distributions and different static allometries of the two species (figure 2*b*; see also Boag (1984)), there is no confusion over the identity of these particular individuals or any others.

When sexes are known, as is the case with specimens collected for museums or birds observed breeding, sex-specific separation of species is slightly more pronounced and the assignment of individuals therefore easier. In all species of ground finches males average 1–4% larger than females in bill dimensions (Price 1984; Grant *et al.* 1985). The Santa Cruz sample of 460 finches was measured outside the breeding season, when growth had probably ceased, but only 52 could be assigned to sex (males) on the basis of black or partially black plumage: 24 *G. fuliginosa*, 23 *G. fortis* and 5 *G. scandens*.

(ii) *The species of finches on Isla Daphne*

Finches on Daphne do not fall into such discrete morphological clusters. Rather, on the same bivariate plot used for the Santa Cruz finches, there are zones of morphological concentration corresponding to the four species on Santa Cruz (figure 3). The problem therefore is one of defining species boundaries in order to classify individuals.

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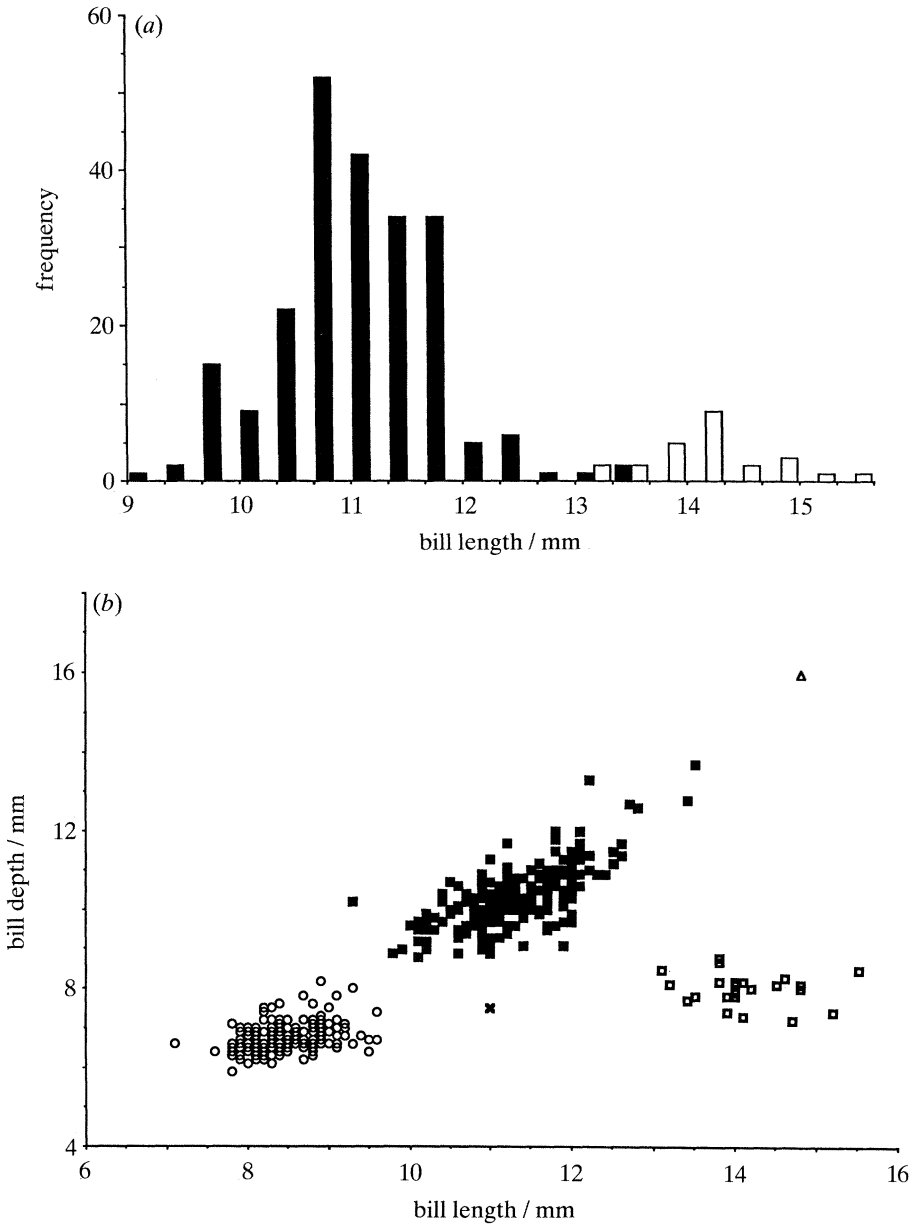

Figure 2. Distributions of bill measurements in millimetres of ground finches at Bahía Borrero, I. Santa Cruz. (*a*) Small overlap in the measurements of *G. fortis* (solid bars) and *G. scandens* (open bars) on one axis. (*b*) Separation of the two species on two bill axes. Symbols for these and two other species are: filled squares, *G. fortis*; open squares, *G. scandens*; open circles, *G. fuliginosa*; open triangles, *G. magnirostris*. × = unidentified individual.

The way in which inbreeding is studied shows how this problem should be addressed. Estimated inbreeding coefficients have meaning only in relation to a base population. The base population, that is the population at the start of a study, is likely to contain an unknown number of inbred individuals and an unknown number of breeding pairs of related individuals. Nevertheless it has to be assumed that members of all mated pairs in the starting (F_0) generation are unrelated (Falconer 1989). The same principle and practice hold for field studies of hybridization when hybrid individuals cannot be unambiguously recognized from their phenotypes (or genotypes) as here. All individuals in the starting generation are assumed to belong to one species or another, and hybrids are assumed to be absent. Morphological criteria developed in the study of finches on Santa Cruz are used to make the initial assignment of individuals to species, as explained below. Pedigrees are then used to determine if species interbreed.

(iii) *Identification of G. scandens*

Most *G. scandens* individuals can be readily recognized by their bill proportions, as on Santa Cruz, but a few individuals are difficult to classify on this basis alone (figure 4). However these individuals are distinctively large in structural size. A principal components analysis (PCA) was performed with the correlation matrix of all six dimensions of all breeding birds that had been banded out of the nest (i.e. their parents were unknown). The sample of 430 birds comprises all

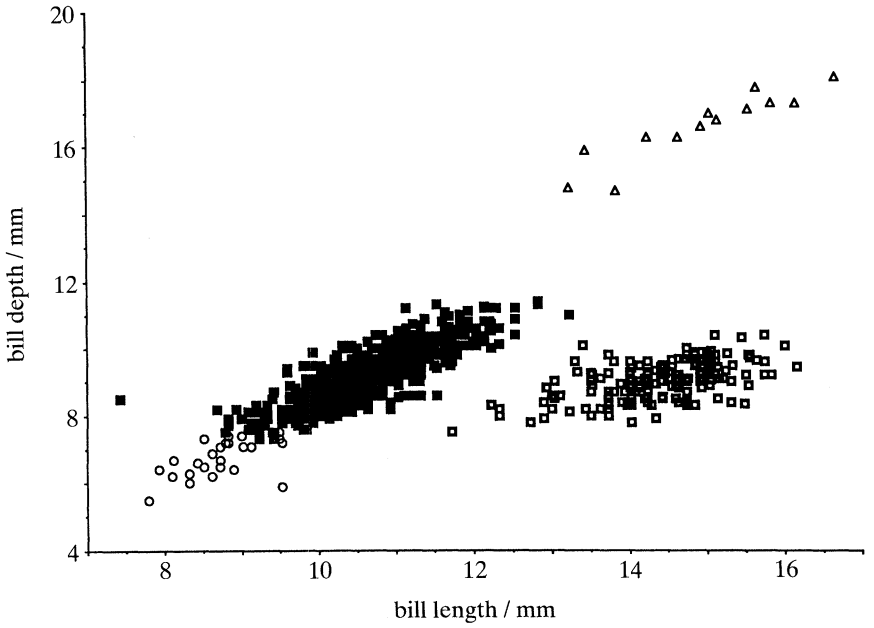

Figure 3. Beak depth plotted against beak length for all measured finches present on Daphne at the beginning of 1976. *G. fortis* and *G. fuliginosa* individuals were distinguished on the basis of a PC analysis (see text and figure 6). Symbols: open circles, *G. fuliginosa*; filled squares, *G. fortis*; open squares, *G. scandens*; open triangles, *G. magnirostris*.

members of the F_0 generation and some members of subsequent generations. The few birds identified in the field by their measurements as *G. fuliginosa* and *G. magnirostris* were not included.

The first component is a size factor, since all of the original variables have strong and positive loadings. It accounts for 64.1% of the original variance. The second component, accounting for a further 24.1%, is a shape factor. Strong and positive loadings for beak depth (0.7803) and width (0.7186) contrast with weaker and negative loadings (down to −0.4229) for all of the other dimensions. On this PC plot *G. scandens* and *G. fortis* are separated by a combination of size and shape factors, and not by either alone. Figure 5 displays the separation of the samples first corrected for sex differences by addition to female measurements of the difference between male and female means (cf. Schluter & Smith 1986). The separation was confirmed by cluster analysis, using NTSYS and a UPGMA method to group individuals according to Euclidean distances between them.

G. fortis individuals are not as easily distinguished from *G. fuliginosa* as they are from *G. scandens*. A different procedure is required.

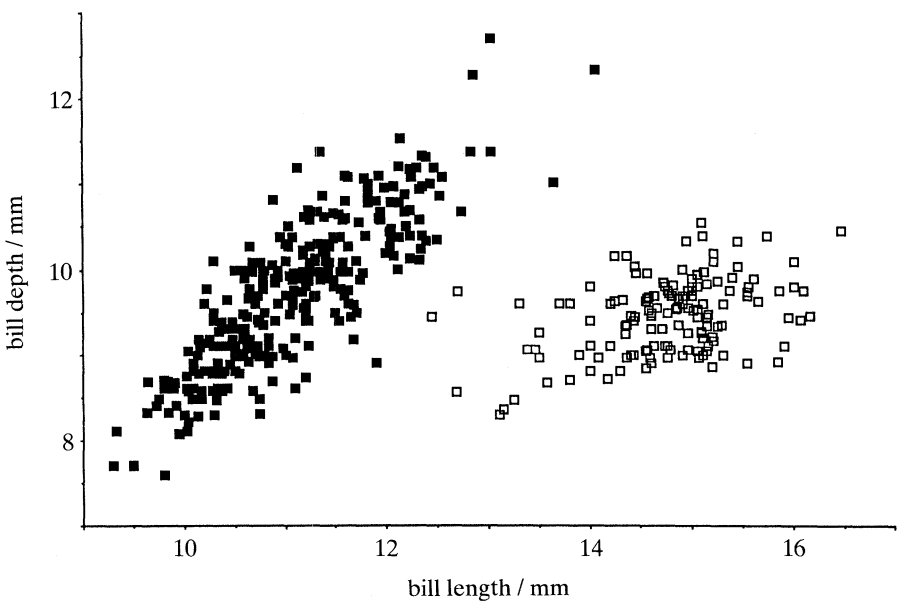

Figure 4. Beak depth plotted against beak length for all measured finches of unknown parents of the two common species that bred on Daphne. Symbols: filled squares, *G. fortis*; open squares, *G. scandens*.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

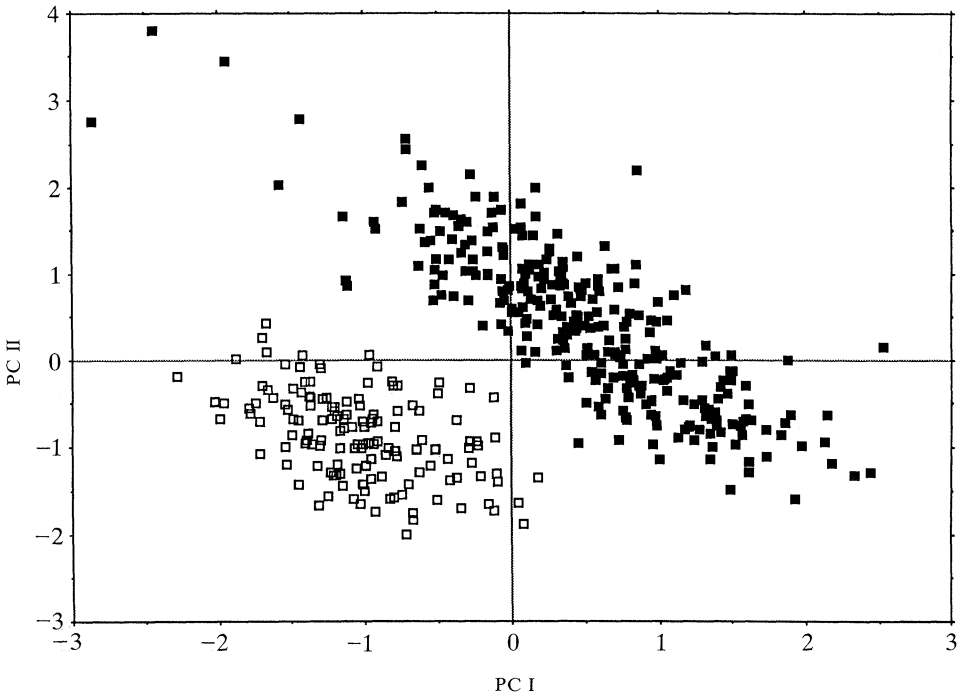

Figure 5. PC analysis of the six dimensions of breeding finches on Daphne. PC I is an axis of overall size, decreasing to the right, and PC II is a bill shape factor, with bills becoming less pointed from bottom to top. Parents of these birds were not known. The same samples are used as in figure 4. Symbols: filled squares, *G. fortis*; open squares, *G. scandens*.

(iv) *Separating* G. fuliginosa *from* G. fortis

Few birds the size of *G. fuliginosa* have bred on Daphne, but many have been present on the island in the non-breeding season. They must have been immigrants. To identify all of them, and not just the breeders, I first deleted *G. scandens* and *G. magnirostris* individuals from the total sample, and then divided the remaining finches into two groups on the basis of bill measurements: into those not distinguishable from *G. fuliginosa* and those distinguishable from *G. fuliginosa* and therefore assigned to *G. fortis*. I used a three-step procedure to exclude birds that could be distinguished from *G. fuliginosa*:

1. Exclude all Daphne birds with a beak depth larger than the largest Santa Cruz *G. fuliginosa* (8.2 mm), and perform a PCA of the three bill measurements of all of the remainder together with the total sample of Santa Cruz *G. fuliginosa*.
2. Exclude all birds with PC I scores beyond that of the largest Santa Cruz *G. fuliginosa*, and perform a second PCA with the remainder.
3. Exclude all birds with PC scores greater than 3.4 standard deviations from the mean of the Santa Cruz *G. fuliginosa*.

The details and reasons are as follows. The first analysis was performed with 697 finches; 208 from Santa Cruz and 489 from Daphne. The two PCs accounted for 95.8% of the variation among individuals in bill dimensions. PC I statistically accounts for the vast majority (87.5%). All dimensions load strongly and approximately equally onto PC I, therefore it is a bill size factor. PC II is a bill shape (pointedness) factor, as bill length loads the most strongly, and positively, and the other two load negatively and approximately equally.

Those Daphne individuals classified as *G. fortis* on the basis of having beak lengths or widths larger than the largest Santa Cruz *G. fuliginosa* were separated from the Santa Cruz birds on the PC I axis. Therefore in the second step all individuals ($n = 111$) more extreme than the largest Santa Cruz *G. fuliginosa* on the first axis were excluded, and another PCA was performed (figure 6) with the remaining 586 birds (208 from Santa Cruz and 378 from Daphne). This gave a similar result to the first PCA. The axes were basically the same (size and pointedness). The total variance explained dropped slightly to 92.4%, and PC I contributed 79.5%.

It is apparent from both analyses that two individuals in the Santa Cruz sample are outliers (figure 6). In the second analysis they were 4.00 and 4.36 standard deviations respectively from the PC I mean. Statistically they are significant outliers ($p < 0.001$, Grubb's test; Sokal & Rohlf 1981). The same is true for their positions in a PCA of the Santa Cruz sample alone; they are 4.03 and 4.26 standard deviations from the PC I mean. Furthermore the distribution of values along this PC I axis is significantly skewed ($g_1 = -0.774$, $p < 0.001$), whereas in a PCA without them there is no significant skewness ($g_1 = -0.238$, $p > 0.1$).

In the second analysis the outliers defined the criterion for exclusion. As a third step I replaced this with a criterion of 3.3 standard deviations either side of the mean PC I and PC II scores for the Santa Cruz sample. The ellipse that connects these points should contain 99.9% of the *G. fuliginosa* individuals. In fact three Santa Cruz individuals are narrowly excluded.

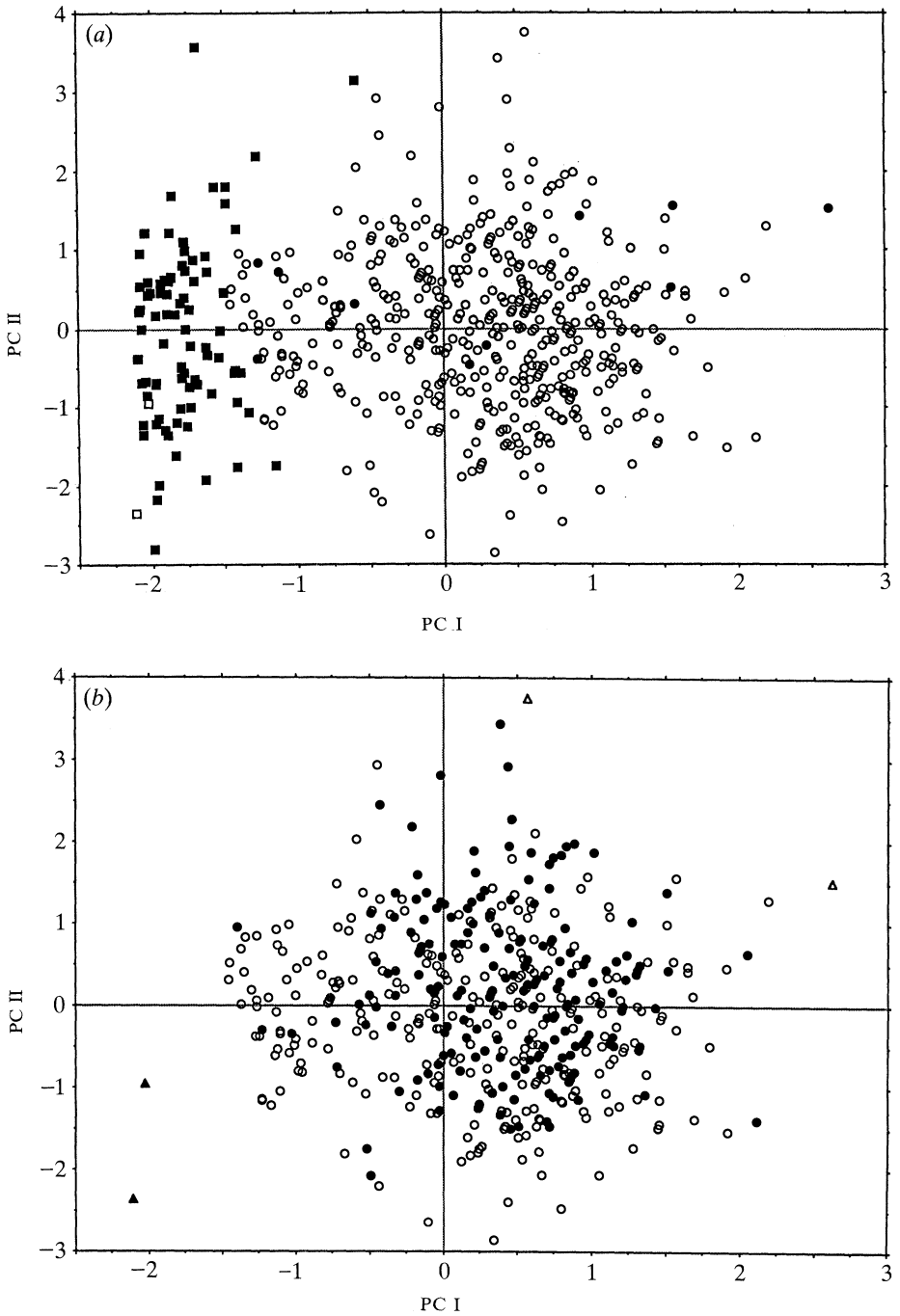

Figure 6. PC analysis of three beak dimensions of *G. fuliginosa* from Bahía Borrero, Santa Cruz island, and small finches on Daphne. Bill size decreases from left to right on the PC I axis, and bill pointedness increases from bottom to top on the PC II axis. (*a*) Individuals identified as *G. fuliginosa* are shown by open circles, and those distinguishable from *G. fuliginosa* and classified as *G. fortis* are indicated by filled squares. The two Santa Cruz outliers are identified by open squares. Ten *G. fuliginosa* that bred on Daphne are identified by filled circles. (*b*) The same plot as above but without the Daphne *G. fortis*. Santa Cruz birds (filled symbols) are contrasted with Daphne birds (open symbols), and outliers are identified by triangles.

Therefore I extended the ellipse to 3.4 standard deviations as this encompasses all of the Santa Cruz sample except for the two large outliers (figure 6).

By this new criterion a further 80 Daphne individuals were excluded. Seven of them were offspring of parents classified as *G. fortis* at step one. None of the offspring of birds classified as *G. fortis* at either of the preceding steps were included in the ellipse.

As a final check on the last step of the procedure two additional PCA were performed. One involved the 506 finches included in the ellipse, and the other involved an additional 20 Daphne birds lying just outside. There was virtually no difference in the results of the two analyses. The axes and the relative positions of the birds on them remained essentially unchanged. Individuals excluded in step three were not repositioned within the cloud of Santa Cruz points.

By this iterative procedure we arrive at a total of 298 finches on Daphne that are morphologically indistinguishable from Santa Cruz *G. fuliginosa*. Two individuals in the Daphne sample fell outside the *G. fuliginosa* ellipse. One is 3.91 standard deviations from the PC 1 mean and *smaller* than all Santa Cruz birds (figure 6*b*). It may have immigrated from another population with a lower mean size than the Santa Cruz population. It may also have suffered stunted growth. The two Santa Cruz outliers may also have suffered stunted growth, in which case they are really members of the *G. fortis* population there, or they may have been hybrids.

Ten measured *G. fuliginosa* individuals bred on Daphne. They are identified in figure 6*a* by solid circles. Their sizes span the full range for the species as represented by scores on the PC 1 axis.

(*b*) *Hybridization*

(i) *Interbreeding*

Breeding took place in 13 of the 17 years in the period 1976–92. *G. fortis* hybridized with *G. fuliginosa* in 11 of those years, and with *G. scandens* in six of them. In addition one *G. scandens* × *G. fuliginosa* pair and one *G. fortis* × *G. magnirostris* pair were formed, but in both cases the nest was abandoned before the eggs were due to hatch (the former pair was incorrectly reported as *G. fuliginosa* × *G. magnirostris* in Grant (1986)). The species and their F_1 hybrids are illustrated in figure 7.

Hybridization was always rare. Hybridizing birds constituted 1.8% of breeding *G. fortis* individuals, on average, and 0.8% of *G. scandens*. Expressed another way, 3.8% of pairs involving *G. fortis* individuals were interspecific pairs, and for *G. scandens* the figure is 1.2%. The highest frequency of interbreeding occurred in 1987 when 4.0% of *G. fortis* individuals and 3.3% of *G. scandens* individuals bred with heterospecific individuals.

A much higher proportion of *G. fuliginosa* individuals hybridized. Seventy three per cent of individuals bred with *G. fortis*, and interspecific pairs constituted 80.0% of those involving *G. fuliginosa*. A large part of the reason for the variation among species in the frequency of interbreeding is the variation in abundance of potential mates. Over the 17-year period harmonic mean breeding population sizes were 198 *G. fortis*, 80 *G. scandens*, and three *G.*

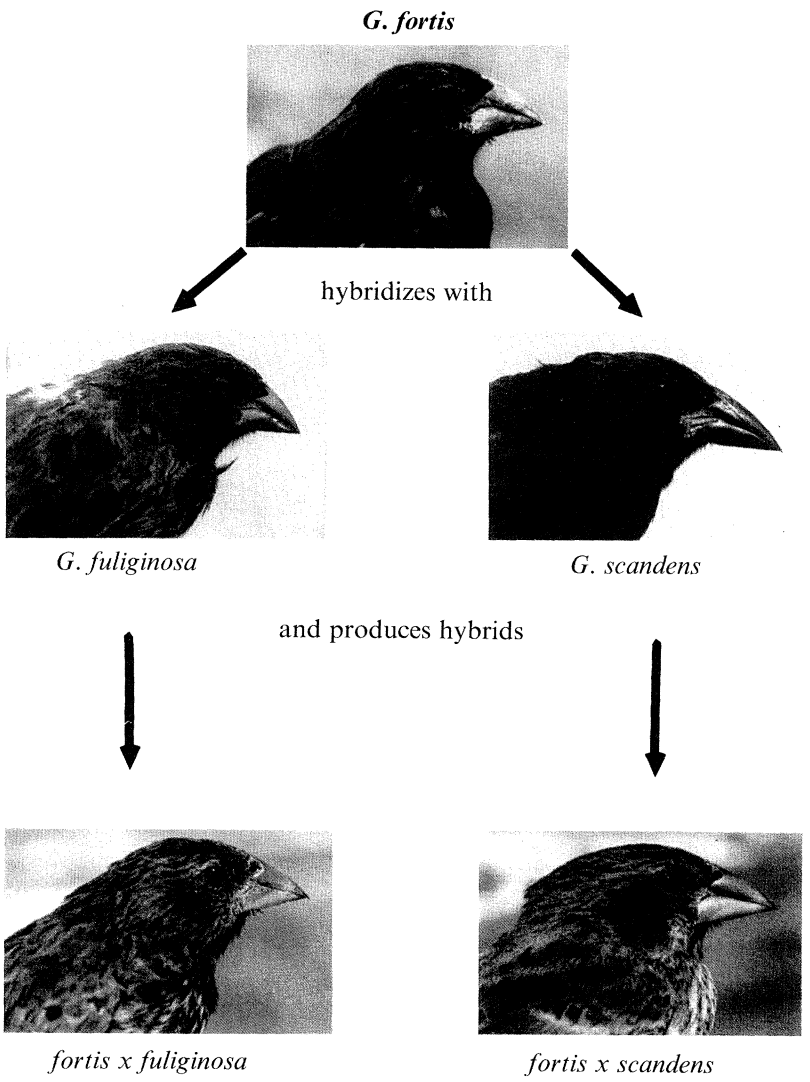

Figure 7. Illustration of hybridizing species and the F_1 hybrids.

fuliginosa, as well as six *G. magnirostris* in the past 10 years only. The relative abundance factor may partly explain the virtual absence of *G. scandens* × *G. fuliginosa* pairs, but not the scarcity of *G. fortis* × *G. magnirostris* pairs. Morphological factors probably play a role in this instance (see, for example, Ratcliffe & Grant (1983)).

Interbreeding was not restricted to the birds ringed out of the nest. Twenty percent of interbreeding *G. fuliginosa* ($n = 28$) were born (hatched) on the island of known parents, and 58.1% of interbreeding *G. fortis* ($n = 45$) and 42.8% of interbreeding *G. scandens* ($n = 7$) were likewise ringed as nestlings.

Some of the original breeders assigned to one species or another were probably F_1 hybrids in the light of subsequent observations of successful interbreeding (see below). Prime candidates are three *G. scandens* males and three *G. fortis* males which sang heterospecific song. Their song was interpreted as evidence of 'misimprinting' (Ratcliffe 1981; Grant 1986). No direct evidence of heterospecific misimprinting has been obtained, therefore it is more likely that these individuals were hybrids. If an equal number of unidentified F_1 females were present the total would be 12. The expected number is a little lower; it is 10, calculated as 2.3% (from table 1) of 453 breeding birds of unknown parents.

Table 1. *Numbers (n) of ringed offspring that fledged; ringed in the nest or, in a few instances, soon after fledging*

species	symbol	*n*	%
fortis	F	4049	60.2
scandens	S	2086	31.0
magnirostris	M	93	1.4
fuliginosa	f	33	0.5
F_1 hybrids			
fortis × *fuliginosa*	F.f	127	1.9
fortis × *scandens*	F.S	28	0.4
F_2 hybrids			
F.f × F.f	Ff.Ff	8	0.1
B_1 backcrosses			
F.f × *fortis*	Ff.F	70	1.0
F.S × *fortis*	FS.F	68	1.0
F.S × *scandens*	FS.S	25	0.4
B_2 backcrosses			
Ff.F × *fortis*	FfF.F	76	1.1
FS.F × *fortis*	FSF.F	23	0.3
FS.S × *scandens*	FSS.S	3	0.1
B_3 backcrosses			
FfF.F × *fortis*	FfFF.F	10	0.1
FSF.F × *fortis*	FSFF.F	6	0.1
others			
F.f × F.S	Ff.FS	4	0.1
FS.F × F.S	FSF.FS	9	0.1
Ff.F × Ff.F	FfF.FfF	3	0.1
Ff.F × FS.F	FfF.FSF	7	0.1
FSF.F × FSF.FS	FSFF.FSFFS	2	0.1
FSF.FfF × *fortis*	FSFFfF.F	1	0.1
totals		6731	100.0

(ii) *The breeding of hybrids*

Hybrids formed from both combinations of parents in each type of cross were fertile as well as viable, and backcrossed to *G. fortis* and *G. scandens* but not to the relatively rare *G. fuliginosa*. A full list of hybrids and backcrosses is given in table 1, and the major pathways of gene exchange are illustrated in figure 8. Table 2 gives the full breeding data down to the level of the second backcross generation. These results demonstrate five major points.

First, males and females of each species hybridized at approximately equal frequency. Exceptions are *G. fortis* males paired with *G. scandens* females, and the backcross class of *fortis–scandens* males paired with *G. fortis* females. The backcross deficiency partly reflects the scarcity of these particular F_1 males, and partly the relatively poor opportunities for breeding when the operational sex ratio is male-biased (Boag & Grant 1984; Grant & Grant 1992*a*). A single *fortis–scandens* F_1 male was alive in 1992. Born (hatched) in 1987, it held a territory from 1990 onwards but failed to attract a mate.

Second, members of the F_2 generation are much rarer than the backcrosses (tables 1 and 2). This can be explained in terms of the scarcity of F_1 hybrids as potential mates for other F_1 hybrids, in contrast to the

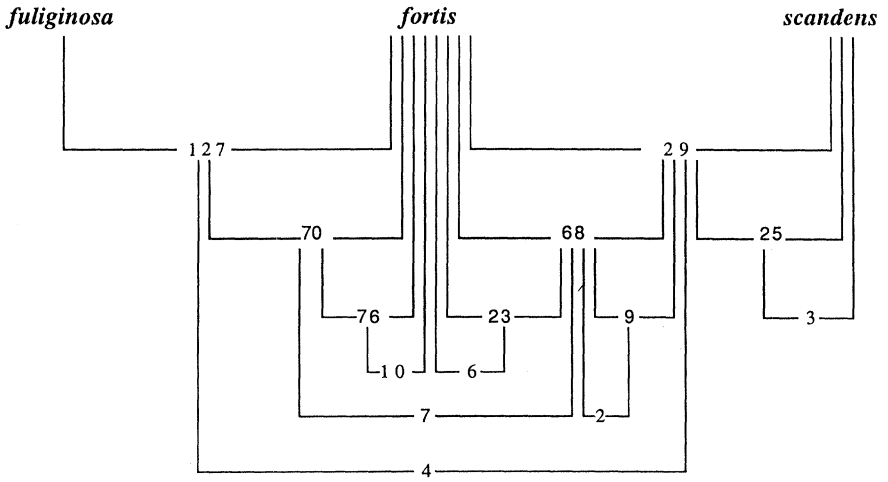

Figure 8. The total number of ringed fledglings produced from 1976 to 1992 by interspecific and various hybrid pairs. A few groups are not shown but are listed in table 1.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 2. *Production of offspring*

(Numbers of birds are given in parentheses. Breeding success is shown as the number of fledglings per clutch of eggs, F/C.)

males		females		pairs	clutch	eggs	nestlings	fledglings	F/C
intraspecific pairs									
fortis	(614)	fortis	(651)	1008	2324	8181	4937	4105	1.77
scandens	(272)	scandens	(288)	472	1251	2922	2637	2039	1.63
fuliginosa	(14)	fuliginosa	(14)	14	27	83	32	32	1.18
interspecific pairs									
fortis	(18)	fuliginosa	(18)	20	37	131	83	71	1.92
fuliginosa	(10)	fortis	(20)	21	39	133	67	55	1.41
fortis	(1)	scandens	(1)	1	2	6	6	1	0.17
scandens	(6)	fortis	(8)	7	18	61	31	27	1.50
hybrid pairs									
f.F	(2)	f.F	(2)	2	4	14	12	12	3.00
backcrossing pairs									
F.f	(6)	fortis	(9)	9	16	48	14	14	0.87
f.F	(3)	fortis	(3)	3	9	27	18	17	1.89
fortis	(2)	F.f	(2)	2	5	18	17	13	2.60
fortis	(12)	f.F	(10)	13	21	69	50	44	2.09
F.S	(1)	fortis	(1)	1	1	4	3	3	3.00
fortis	(8)	F.S	(4)	9	25	92	57	50	2.00
scandens	(6)	F.S	(3)	6	12	43	31	27	2.25
backcrosses									
Ff.F	(9)	fortis	(9)	9	22	73	42	39	1.77
fortis	(8)	Ff.F	(6)	8	23	81	63	52	2.26
FS.F	(7)	fortis	(7)	7	14	43	23	18	1.29
fortis	(2)	FS.F	(2)	2	5	19	12	12	2.40

relative abundance of potential mates among *G. fortis* and *G. scandens* individuals.

Third, there is no evidence of an absolute barrier to the exchange of genes between species (table 2), except possibly between *G. fortis* and *G. magnirostris*, and between *G. fuliginosa* and *G. scandens*. Because the nests in these two exceptional cases were abandoned before the eggs were due to hatch, as many nests are, their failure does not unambiguously show an inability to interbreed. In all other cases at least one fledgling was produced by every combination of breeders that succeeded in starting a clutch.

Fourth, although partial barriers to gene exchange could exist in the form of genetic incompatibilities which are manifested in the F_1, F_2 or backcross generations, the compilation of breeding data in table 1 provides little evidence of any such incompatibilities. Interspecific pairs do not have noticeably lower hatching success or fledging success than intraspecific pairs (table 2). F_2 generation offspring were produced from only two F_1 pairs, but hatching and fledging success were high (table 2). Incompatibilities may be anticipated when the heterogametic sex (females) in backcrossing pairs is a hybrid (see Coyne & Orr 1989). This is certainly not shown by pairs involving *fortis–fuliginosa* hybrids, whereas a weak difference in the expected direction is observed in the small sample of pairs involving *fortis–scandens* hybrids (table 2). A more detailed and statistical analysis that allowed for the marked annual variation in breeding performance failed to find evidence of a reproductive disadvantage to interspecific or hybrid pairs (Grant & Grant 1992*b*).

Fifth, despite the absence of successful interbreeding between *G. fuliginosa* and *G. scandens*, genes may pass from *G. fuliginosa* to *G. scandens* through *G. fortis* as an intermediary, as each of them hybridizes with *G. fortis*, and the hybrids backcross to *G. scandens* (figure 8). The *G. fortis* population harbours genes from the other two species.

A final ancillary point concerns the classification of small birds, and the likelihood that a few of those classified as *G. fuliginosa* were hybrids. Twenty-four (8.1%) of the 298 birds not distinguishable from *G. fuliginosa* are known from the pedigrees to be hybrids. Fifteen were F_1 hybrids of *G. fortis* and *G. fuliginosa*, one was an F_2 hybrid, four were members of the first generation of backcrosses to *G. fortis*, and three were members of the second generation of backcrosses. The remaining bird was produced by a *fortis–scandens* F_1 hybrid backcrossing to *G. fortis*. Therefore some of the breeders classified as *G. fuliginosa*, particularly those (four) closest to *G. fortis* in morphology, may have been hybrids. Most hybrids, however, were produced by the smallest *G. fuliginosa* individuals, and so any misclassification that might have occurred is is unlikely to have had a major effect on the results.

4. DISCUSSION

The results of this study show that hybridization occurs in Darwin's finches at a low frequency. A

shorter study on Isla Genovesa produced a similar finding. *G. conirostris* hybridizes there with *G. magnirostris* and *G. difficilis* at a frequency of about one percent (Grant & Grant 1989). Beak dimensions of more than a dozen populations of different species of Darwin's finches are unusually variable (Grant *et al.* 1985), and this has been interpreted as indirect evidence of hybridization (Grant & Price 1981). Therefore it is likely that some, if not all, of the so-called freak specimens in museum collections which have stimulated much discussion about the possibility of hybridization (Lack 1945, 1947; Bowman 1961; Vagvolgyi & Vagvolgyi 1990) are indeed hybrids.

It is not known why Darwin's finches hybridize, why only a few individuals do, and why those particular individuals do. Morphological analysis suggests that phenotypic similarity of the interbreeding individuals is one factor (P. R. Grant, unpublished observations), and demographic study shows that a biased sex-ratio is another (Grant & Grant 1992*a*). In contrast to causes, several consequences have been determined. The present study, coupled with a morphological analysis of the hybrids, shows that genes can pass between populations. It does not address the question of how fit the hybrids are in relation to non-hybrids. An extension of this study shows that relative fitness of hybrids depends on ecological conditions (Grant & Grant 1992*b*; B. R. Grant & P. R. Grant 1993). Under relatively dry conditions when the biomass of large and hard seeds predominates in the food supply, as happened in the first half of the study, hybrids are at a strong disadvantage. None of those born (hatched) in the years 1976–82 bred before 1983, and most died without having had the opportunity to breed. When the biomass of small-soft seeds predominates, as occurred in the years following the exceptionally wet year of 1983, the relative fitness of hybrids is equal to or greater than the relative fitness of the parental species as a result of their high survival. Thus ecological factors are at least as important as genetic factors in determining the relative fitness of hybrids.

(*a*) *Hybridization and the origin of new forms*

The demonstration of backcrossing and of high hybrid fitness under some conditions on Daphne makes it logical to consider hybridization as a potentially important evolutionary force that influenced the diversification of the group. The hybrid segregation hypothesis of Bateson and Lowe, a mendelian hypothesis, is too simple an explanation for the evolution of that diversity, and not supported by either ecological (Grant 1986) or geological (e.g. Cox 1983) evidence. Nevertheless hybridization may have been influential in other ways (B. R. Grant & P. R. Grant 1993).

Lack first attributed the intermediate size of *G. fortis* to hybridization with *G. fuliginosa* (Lack 1945), noting that occasional individuals of this second species have been observed and collected on Daphne (in addition, see Harris (1973)). Lack abandoned the idea in favour of an ecological explanation for the intermediate appearance of *G. fortis* on Daphne upon realizing that the explanatory power of Gause's competitive exclusion principle applied to the evolution of Darwin's Finches as a whole (Lack 1947). Recently Vagvolgyi & Vagvolgyi (1990) have urged a return to Lack's original position, favouring, as did Lack, a single factor explanation for a complex phenomenon (see, for example, Mayr (1974)). In fact the two hypotheses are not necessarily in opposition.

Ecological factors (Schluter *et al.* 1985), combined with directional selection on beak size (Boag & Grant 1981; Price *et al.* 1984; Gibbs & Grant 1987*b*), can account for mean beak and body size traits in this population, but hybridization and backcrossing have additional, small, directional effects upon those trait means (P. R. Grant & B. R. Grant 1993). One reason why these additional effects are small is that hybridization is rare. Another reason is that *G. fortis* hybridizes not only with the smaller *G. fuliginosa* but with the larger *G. scandens*. Thus the directional effects of one tend to cancel the effects of the other. On the other hand hybridization with both species supplies new genetic variation upon which selection acts, thereby facilitating evolutionary change (Grant & Price 1981; Boag & Grant 1984; Price, Grant *et al.* 1984). This last factor could have been important in the diversification of the group, contributing to the relatively rapid rate at which the radiation occurred (Grant 1986). Other evolutionary effects of hybridization, enhancing or retarding diversification, have been discussed elsewhere (Grant & Grant 1992*b*, P. R. Grant & B. R. Grant 1993).

In conclusion, the two issues raised in the Introduction have been resolved. Hybridization of Darwin's finch species does occur in nature. Although it is not the only factor, hybridization contributes to the morphologically intermediate appearance of certain populations to a small degree. Interestingly, hybridization has recently been found in related birds in a related setting. *Nesospiza* (bunting) species hybridize on the remote and largely undisturbed Inaccessible island in the Tristan da Cunha group, and as a result display high levels of morphological variation (Ryan 1992).

(*b*) *Hybridization and the concept of species*

The demonstration of natural hybridization answers some questions but raises others. In particular the demonstration of hybridization and backcrossing without impaired fertility (Grant & Grant 1992*b*) exposes the problem of defining and recognizing a species. It is a general problem without a general solution.

Species of sexually reproducing organisms have been defined as 'groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups' (Mayr 1963). Mayr's (1970) later modification allows for the fact that two populations may exchange genes through the interbreeding of some of their members, regularly or episodically, yet remain distinctive phenotypically and genetically through the selective elimination of some of the exchanged genes.

An alternative version of this biological species concept is founded on a literal interpretation of the reproductive isolation criterion. According to this a

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

species comprises populations which exchange genes through interbreeding but which do not form fertile hybrids with others (Bigelow 1965; Key 1968; Barton & Hewitt 1985). Because backcrossing and not interbreeding is the criterion of inclusion or exclusion, this can be thought of as both a concept and a definition of species based on the principle of genetic isolation. Mayr's concept is broader, encompassing both complete and partial genetic isolation, but is not easy to apply when the genetic isolation is partial. According to a third view, referred to as the phylogenetic species concept, a species is a cluster of organisms diagnosably distinct from other such clusters and within which there is a pattern of ancestry and descent (McKitrick & Zink 1988; Cracraft 1989). Other views have been discussed recently by Endler (1989), Templeton (1989), Coyne *et al.* (1988), White & Michaux (1990) and others.

Despite recent efforts to devise a unifying concept for all species (Templeton 1989), none has met with universal success (Endler 1989). Different concepts are appropriate for different purposes. Where the chief concern is phylogenetic reconstruction and classification the phylogenetic species concept finds favour. Where the main concern is on genes and their flow through populations the complete genetic isolation concept is preferred. Where the principal interest is the ecological performance and evolutionary fate of populations, as here, Mayr's concept of partial or complete reproductive isolation is often found to be most useful.

The choice of a concept determines the number of species recognized when interbreeding occurs. If the complete genetic isolation concept were to be adopted we would recognize only two species of Darwin's finch on Daphne, despite the strong morphological differences among four, assortatively mating, rarely interbreeding groups (populations) of birds. The three populations of ground finches on Genovesa (Grant & Grant 1989) would similarly be reduced to one species. In fact there would be grounds (hybridization: Grant 1986) for fusing all six species into one, and reducing the number of species in other Darwin's finch genera for the same reasons. At the extreme, six species would be recognized in place of the current 14, and additional study might necessitate yet further reduction. Application of the phylogenetic species concept would result in recognition of a similar small number.

The issue is made more complex by apparent variation among islands in the degree to which populations interbreed. *G. fortis* coexists with *G. fuliginosa* on 15 islands in the archipelago and with *G. scandens* on 14 of them (Grant 1986). Coexisting species are usually morphologically distinct and apparently do not interbreed, although none of the species has been studied in as much detail as on Daphne and so rare hybridization could have escaped detection. It is particularly likely to occur on Santa Cruz and Santiago where the species are similar in morphology (Snow 1966; Ford *et al.* 1973) and protein polymorphisms (Yang & Patton 1981). This situation, of hybridization at one or a few locations but not at others, is not unique to these finches (for examples, see Meise (1936); Sibley & Sibley (1964)), or to birds (Fox 1951; Wake *et al.* 1986).

The complete fusion of *G. fortis* and the other two species with which it rarely breeds on Daphne would take more than a century under unaltered conditions (Boag & Grant 1984). However the climate fluctuates markedly, on the scale of a decade or less, causing changes in the vegetation and in the food supply of finches (Gibbs & Grant 1987*a*,*b*; B. R. Grant & P. R. Grant 1993). As a consequence natural selection occurs intermittently, oscillating in direction, and hybrid relative fitness fluctuates, so it is doubtful if fusion is taking place. Thus in terms of the broad biological concept of species, which is adopted here, there are four species on Daphne, neither completely independent evolutionarily on the one hand (except for *G. magnirostris*), nor approaching panmixia on the other. This conclusion leaves unchanged the modern classification of Darwin's finch populations into 14 species, without removing the doubts about a few populations for the quite different reason that they are allopatric, and hence do not have the chance to interbreed even if capable of doing so (Grant 1986).

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G. fortis

hybridizes with

G. fuliginosa

G. scandens

and produces hybrids

fortis x fuliginosa

fortis x scandens

Figure 7. Illustration of hybridizing species and the F_1 hybrids.