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Evolution of Darwin's finches caused by a rare climatic event

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SUMMARY

Populations of animals and plants often undergo conspicuous ecological changes when subjected to climatic extremes. Evolutionary changes may accompany them but are less easily detected. We show that Darwin's finches on a Galápagos island underwent two evolutionary changes after a severe El Niño event caused changes in their food supply. Small beak sizes were selectively favoured in one granivorous species when large seeds became scarce. The effects of selection were transmitted to the next generation as a result of high trait heritabilities. Hybridization between this species and two others resulted in gene exchange, but only after the El Niño when hybrid fitness was much enhanced under the altered feeding conditions. These observations imply that if global warming increases the frequency or severity of El Niño events on the Galápagos, microevolutionary changes in animal and plant populations are to be anticipated.

1. INTRODUCTION

The distribution and abundance of terrestrial organisms are influenced by many factors including climate. When the climate changes, between seasons or years, ecological changes in populations are often observed. Less obvious are the evolutionary changes that may accompany them. Yet over long periods of evolutionary time adaptations arise and become fixed for various ways of coping with climatic extremes or fluctuations, such as diapause, migration, hibernation, aestivation and the timing of growth and reproduction. If climatic factors are so important in determining major features of evolution, we should be able to detect the influence of climate on microevolution in contemporary time.

Modern evidence for this influence falls into three groups. First, genotypes which have an advantage under stressful climatic conditions have been identified in *Drosophila* flies (Hoffman & Parsons 1989), *Colias* butterflies (Watt 1977), *Adalia* beetles (Creed 1975), *Cepaea* snails (Richardson 1974, Cameron 1992), and several species of plants (Endler 1986). Second, gene frequencies vary in space, often clinally, and associations have been established between microgeographical variation in climate, in phenotype, and in underlying genotype (Jones 1970; Jones *et al.* 1977). Third, natural selection has been studied directly in the wild, and in a few cases climatic factors have been identified as probable causal agents (Endler 1986).

Adaptation is constrained by the amount and type of genetic variation exposed to selection. Persistent directional selection is expected to erode genetic variation, whereas mutation and introgression will replenish it. Lewontin & Birch (1966) argued from experimental data on fruit flies (*Dacus*) that hybridization could enhance adaptation to extreme climatic conditions through the production of novel genotypes. Thus two evolutionary forces, selection and hybrid-

ization, may work serially or in tandem rather than in opposition, and result in major evolutionary changes. Both are the focus of this paper. Populations of Darwin's finches have been studied continuously from 1976 to 1991 on the small (0.34 km²), uninhabited and undisturbed Galápagos island of Daphne Major. A large perturbation to the climate altered the plant composition on the island. This created new selection pressures on one of the finch species, resulting in a microevolutionary change. It also changed the outcome of hybridization with two other species.

2. ECOLOGICAL EFFECTS OF A CLIMATIC DISTURBANCE

In 1982–1983 an exceptionally strong El Niño event occurred. Starting in November 1982 and lasting to July 1983, it was the most severe oceanographic and climatic disturbance in the Pacific region of the century (Cane 1983), possibly the most severe in 400 years (Glynn 1990). It brought heavy rains to the Galápagos for eight months (Gibbs & Grant 1987*a*; Grant & Grant 1987). For comparison, the next event four years later (figure 1) was more typical in lasting for four to five months.

Most Galápagos islands are low lying, experience seasonally arid conditions and support drought-adapted communities of plants. Effects of abundant rainfall in 1982–83 on these communities were profound throughout the archipelago (Robinson & del Pino 1985). Changes in plant communities caused changes in the granivorous finch populations.

On Daphne Major island a dramatic switch occurred from large–hard seeds to small–soft seeds shortly after the 1982–1983 El Niño event (figure 2). At the sampling times in 1983, vegetation was growing rapidly and seed biomass was relatively low (figure 2). Annual

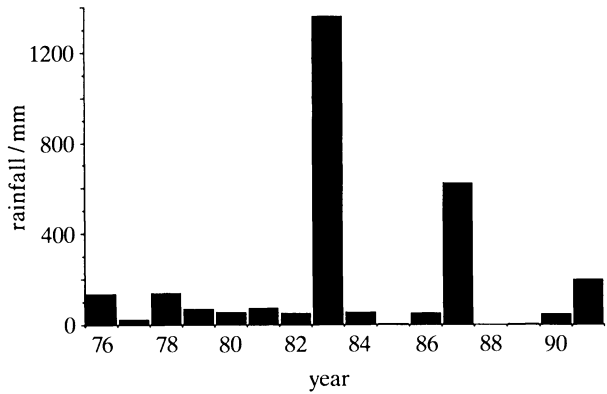


Figure 1. Annual fluctuations in rainfall on Daphne Major island from 1976 to 1991. Rainfall in November and December 1982 has been included in the 1983 total (no rain fell in these two months in any other year). Rain typically falls in the months January–April.

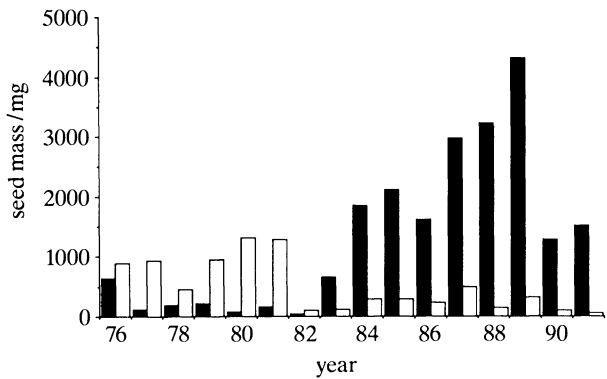


Figure 2. Temporal variation in the biomass of seeds in the smallest and largest classes categorized by size and hardness. Values are mean wet mass (in milligrams) per square metre. The seed supply on Daphne Major island was sampled twice a year from 1976 to 1991. Methods are described in Boag & Grant (1984a). All seeds were counted and identified in 50 lm^2 quadrats randomly chosen each sampling time in a permanent grid of 5000 m^2 . Annual totals for each seed species were converted to biomass by multiplying by the mean wet mass. Seeds are classified by an index of size and hardness, which are of significance to the finches because they must crack the hulls to extract the kernels. Size (in millimetres) is the largest dimension of the whole seed or woody fruit at right angles to its length. Hardness is the force (in newtons) required to crack the seed. These are combined in an index by taking the geometric mean. Of the 26 seed species recorded in the samples, 24 are eaten by finches. They fall into three discrete size–hardness classes. There are 20 species which contribute to the small–soft category (index < 6; filled bars), whereas *Tribulus cistoides* is the only species in the large–hard category (index 27; open bars). The third class (index 7–12), not shown, comprises *Opuntia echios*, *Bursera graveolens* and *Cenchrus platyacanthus* seeds; the last two are consumed as they ripen and contribute little to the dry season food supply. Mean biomass of small–soft seeds was $206.14 \text{ mg} \pm 76.74$ (s.e.m.) per square metre in the seven years before the 1983 El Niño event, and 2441 ± 361.49 mg in the eight following years. Mean biomass of large–hard seeds was 843.89 ± 165.07 mg before 1983 and 244.66 ± 50.96 mg afterwards.

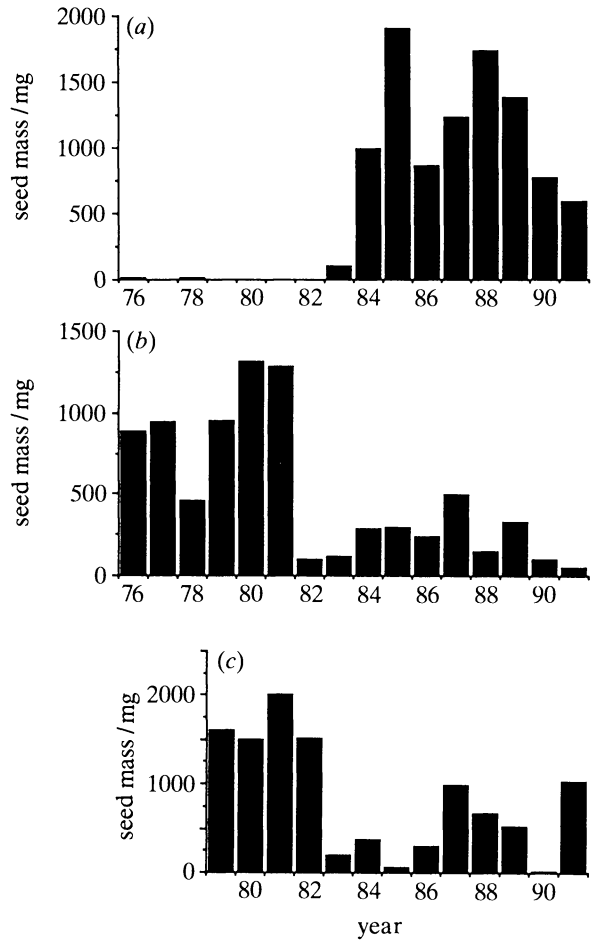


Figure 3. Changes in the seed abundances of (a) *Cacabus miersii* (small), (b) *Tribulus cistoides* (large) and (c) *Opuntia echios* (medium). Mean size–hardness values are 2, 27 and 10, respectively. *Cacabus* and *Tribulus* seed abundances were estimated from randomly sampled quadrats (figure 2). *Opuntia* seed abundances were estimated from ten marked bushes censused each week (see text). They are concordant with estimates from the quadrats, but are more precise.

biomass of large and hard seeds (*Tribulus cistoides*) was significantly lower in eight years after 1983 than in the seven preceding years (ANOVA, $F_{1,13} = 13.67$, $p = 0.003$), whereas the collective biomass of all small seeds significantly increased after 1983 ($F_{1,13} = 28.40$, $p < 0.001$). Total annual biomass of seeds was also higher after 1983 than before ($F_{1,13} = 11.23$, $p = 0.005$).

Biomass of small seeds after 1983 was dominated by *Cacabus miersii*, which was scarcely detectable in the samples before 1983 (figure 3). *Tribulus cistoides*, a prostrate perennial, declined in seed production in 1982, possibly because it was attacked by a rust, but in 1983 and later years it was smothered by *Cacabus*, vines and other plants. *Opuntia echios*, the prickly pear cactus, was also smothered by other plants. Annual fruit production of ten marked *Opuntia* bushes was significantly lower in the eight years after 1983 than in the immediately preceding four years (repeated measures ANOVA, $F_{1,10} = 29.31$, $p < 0.001$).

All these seeds are eaten by Darwin's finches. Two species are resident on the island: *Geospiza fortis*, the medium ground finch (mass ≈ 17 g), and *G. scandens*, the cactus finch (≈ 21 g). Individuals of two other

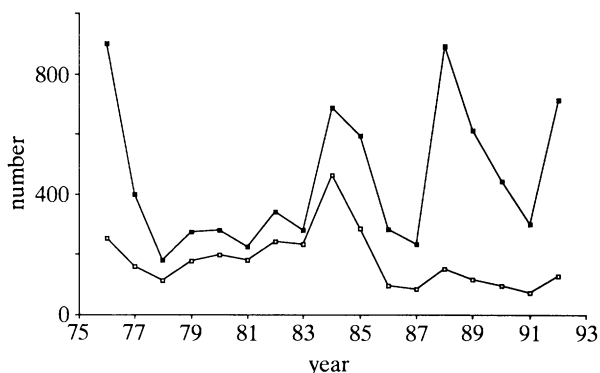


Figure 4. Numbers of *Geospiza fortis* (filled symbols) and *G. scandens* (open symbols) alive on Daphne in January of each year. Harmonic population sizes of breeding birds over the period 1976–1991 were 197 *G. fortis*, 94 *G. scandens* and (not shown above) 6 *G. fuliginosa* (Grant & Grant 1992a).

species, *G. fuliginosa*, the small ground finch (≈ 13 g), and *G. magnirostris*, the large ground finch (≈ 28 g), immigrate from the neighbouring large island of Santa Cruz in most years, and a few stay to breed (Grant 1986). The El Niño event of 1982–1983 had two ecological effects upon the finches (Gibbs & Grant 1987a). The first, direct, effect was to prolong favourable conditions for breeding. Individual finches produced up to eight broods in eight months, and birds born at the beginning of the season bred, some

successfully, in the second half (Gibbs *et al.* 1984). The second, indirect, effect was an alteration in the relative abundance of the two species. Most mortality normally occurs in the dry season (Gibbs & Grant 1987b) when *G. fortis* feeds in a generalist manner on seeds of various sizes and *G. scandens* largely specializes on *Opuntia* seeds (Boag & Grant 1984a). The effect of a change in seed abundance and composition was to depress the numbers of *G. scandens*, both absolutely and relative to *G. fortis* numbers. In the dry conditions prevailing after 1983, *G. scandens* numbers fell to a lower level (in 1986) than at any time in the preceding decade, and by 1991 numbers were even lower (figure 4). The most important factor was probably the decline in *Opuntia* cactus abundance.

3. NATURAL SELECTION

The change in seed composition associated with the El Niño event of 1982–1983 altered selection pressures on *G. fortis*. Breeding occurred in the moderately dry year of 1984 (53 mm of rain), but not in 1985 (4 mm), and almost none occurred in 1986 (49 mm; four fledglings produced). Populations declined (figure 4). From 1984 to the beginning of 1986, mortality of *G. fortis* was size selective. Small birds survived best, and selection gradient analysis (Lande & Arnold 1983) identified bill width as a target of selection (Gibbs & Grant 1987c). Table 1 gives the results of an analysis of selection over the longer period of 1984 to 1987, that is,

Table 1. Standardized selection differentials (s) and gradients (β) for *Geospiza fortis* and *G. scandens* from 1984 to 1987

(Values of β are shown \pm s.e.m. Most measurements were made by P. R. G. Correction factors for the remainder were calculated from birds measured by P. R. G. and other measurers. Measurements were taken from 53% of *G. fortis* and 49% of *G. scandens* alive in 1984 (before selection). Of those that survived to breed in 1987 (after selection), 99% of *G. fortis* and 98% of *G. scandens* were measured. Before each analysis data were \log_e -transformed and standardized to have zero mean and unit variance. Principal component (pc) scores were extracted from a correlation matrix calculated from all individuals for which measurements of all six univariate traits were available. pc I is interpreted as a measure of overall body size because all characters load positively and approximately equally on it, whereas pc II is interpreted as a shape index in terms of bill size relative to tarsus length; n is the number of birds alive at the beginning of the period, and varies according to the number of measurements taken. The proportion surviving is given in parentheses. Significance of selection differentials and gradients was assessed by t -tests. Significance of the gradients was confirmed by t -tests of the coefficients from a logistic regression analysis. The gradients were robust to the serial deletion of body-size traits. For the differentials, 1987 breeders were compared with non-survivors (386 *G. fortis*, 244 *G. scandens*) combined with those which failed to breed (3 *G. fortis*, 22 *G. scandens*). *G. fortis* bill depth was omitted from the gradient analysis because it is strongly correlated ($r = 0.857$) with bill width, and the repeatability of measurements is lower for bill depth (0.94) than for bill width (0.98) (Boag 1983). All other correlations for *G. fortis* traits are < 0.68 , and for *G. scandens* all correlations are < 0.77 . (F_1 hybrids ($n = 26$) were excluded from the analyses.)

	<i>G. fortis</i>		<i>G. scandens</i>	
	s	β	s	β
mass	-0.11	-0.05 ± 0.10	0.19	0.15 ± 0.19
wing	-0.08	-0.02 ± 0.08	0.14	0.13 ± 0.18
tarsus	-0.09	-0.04 ± 0.08	0.15	0.04 ± 0.16
bill length	-0.03	0.20 ± 0.09^a	0.16	0.13 ± 0.16
bill depth	-0.16 ^a	—	0.06	-0.22 ± 0.22
bill width	-0.17 ^a	-0.24 ± 0.09^b	0.12	0.08 ± 0.21
pc 1	-0.12	—	0.19	—
pc 2	0.06	—	0.14	—
n	552–566	552 (0.32)	308–325	308 (0.17)
r^2	—	0.02 ^a	—	0.02

^a $p < 0.05$.

^b $p < 0.01$.

up to the time when the whole population responded to rainfall by breeding for the first time since 1984. Only 32% survived to breed in 1987.

The population underwent a shift in beak size during this time. Beak depth and width were significantly smaller among the survivors than among non-survivors. These two traits are so highly correlated (table 1) they may be considered a single trait. Therefore, only one of them, bill width, was entered into a multiple regression analysis of fitness (survival) in relation to morphological traits. Two variables had significant entries in the resulting selection gradient. Bill width was selected to decrease, as expected from the selection differential, and bill length was selected to increase. Selection on bill length was revealed when the masking influence of the positively correlated bill width was removed. The net effect was to alter beak width but to leave beak length unchanged.

The selective shifts are accounted for by ecological and behavioural factors. Responding to a change in composition of the seed supply (figures 2 and 3), the *G. fortis* population fed to a significantly greater extent on small seeds in the eight years after 1983 than in the seven years before (ANOVA, $F_{1,13} = 40.82$, $p < 0.001$, with arcsine-transformed proportions), and to a significantly lesser extent on *Tribulus* seeds ($F_{1,13} = 8.29$, $p = 0.01$) and *Opuntia* seeds ($F_{1,13} = 15.98$, $p = 0.002$). The analysis was restricted to ringed birds ($n = 1526$), and the first observation per bird per year. Other analyses using proportions of the three seed types in the diets of known individuals gave the same results.

Although diets closely reflect food availability, and hence can change by individuals altering their behaviour, some variation in diet is statistically explicable in terms of beak size. This is shown by the results of a multiple regression analysis of arcsine-transformed proportions of small seeds in the diet of 175 finches observed feeding at least ten times over one or more years in the period 1978–1991. Independent variables, \log_3 -transformed and standardized, were small seed abundance, beak width and beak length. The R^2 value of the regression was 0.73 ($p < 0.001$). Standardized regression coefficients were significant for small seed abundance (0.55 ± 0.03 , $p < 0.001$) and beak width (-0.19 ± 0.04 , $p < 0.001$) but not for beak length (0.01 ± 0.04 , $p > 0.1$). Mechanical efficiency of handling small seeds appears to be a feature of finches with small beaks (Bowman 1961; Schluter 1982).

G. scandens remained specialists on *Opuntia* seeds. They did not undergo dietary shifts, and those that bred were not a selected group, therefore no evolution is predicted in this species.

4. EVOLUTION

Evolution occurs when the effects of selection on a heritable trait in one generation are transmitted to the next generation. Evolution of *G. fortis* as a result of directional selection is to be expected because beak traits are highly heritable; heritability values are 0.65 for beak length and 0.90 for beak width (Boag 1983). When selection occurs independently on two (or more) traits, an evolutionary response is predicted on the

basis of the strength of selection on each trait (b_i, b_j), the genetic variance of each trait (G_i, G_j), and the genetic covariance between the traits (G_{ij}) (Lande 1979). Thus for *G. fortis*:

$$\Delta \text{beak length} = \Delta \bar{x}_1 = b_1 G_{11} + b_2 G_{12} \quad (1)$$

$$\Delta \text{beak width} = \Delta \bar{x}_2 = b_2 G_{22} + b_1 G_{21}, \quad (2)$$

assuming no selection on any other correlated trait. Numerical solutions to the equations are obtained by using genetic parameters, estimated from offspring-parent resemblances determined in 1976 and 1978 (Boag 1983), and β values in table 1:

$$\Delta \text{beak length} = 0.068 - 0.067 = 0.001$$

$$\Delta \text{beak width} = -0.071 + 0.058 = -0.013$$

The first term on the right-hand side of each equation represents the direct response to selection on the trait, and the second term represents the indirect response arising from the direct effect of selection on a genetically correlated trait. For beak length the two terms are almost equal and of opposite sign, and therefore virtually no response is predicted. For beak width the direct response component is stronger than the indirect one, and a decrease in mean is predicted.

Observed responses closely match these predictions, and are measured by the difference between the population mean of a trait before selection and the mean of the trait in the next generation; in this case it is the difference between the mean of those alive in 1984 and the mean of those born in 1987 (when fully grown). The mean beak length of *G. fortis* is predicted to increase from 10.92 mm to 10.93 mm, i.e. virtually no change. In fact it increased to 10.98 mm, which is, however, not significantly different from the 1984 mean ($t_{999} = 1.44$, $p < 0.1$). Mean beak width is predicted to decrease from 8.86 mm to 8.74 mm. This is exactly what was observed, and the difference is highly significant ($t_{1000} = 3.38$, $p < 0.001$). *G. scandens* dimensions are not predicted to change, and in agreement with this prediction the 1987 offspring means did not differ from the 1984 means (t tests, $p > 0.01$).

No further directional selection took place after 1987, and hence no further evolution occurred. Although mortality was high in association with post-El Niño drought conditions (figure 4), it was not size selective in any of the four years after 1987 (t tests, $p > 0.1$ in all cases), during which period seed composition remained the same (figure 2).

These results complement an earlier demonstration of selection for large size in the drought year of 1977 when the supply of small seeds declined both absolutely and in relation to the supply of large seeds (figure 2) (Boag & Grant 1981; Price *et al.* 1984). The expected increase in size in the next generation was observed (Boag 1983), although it was not assessed with the predictive equations for multivariate evolution used here.

5. HYBRIDIZATION

Hybridization occurred throughout the study, in 10 out of 12 breeding seasons, but was always rare; the frequency of interspecific pairs was 0–4% (Grant &

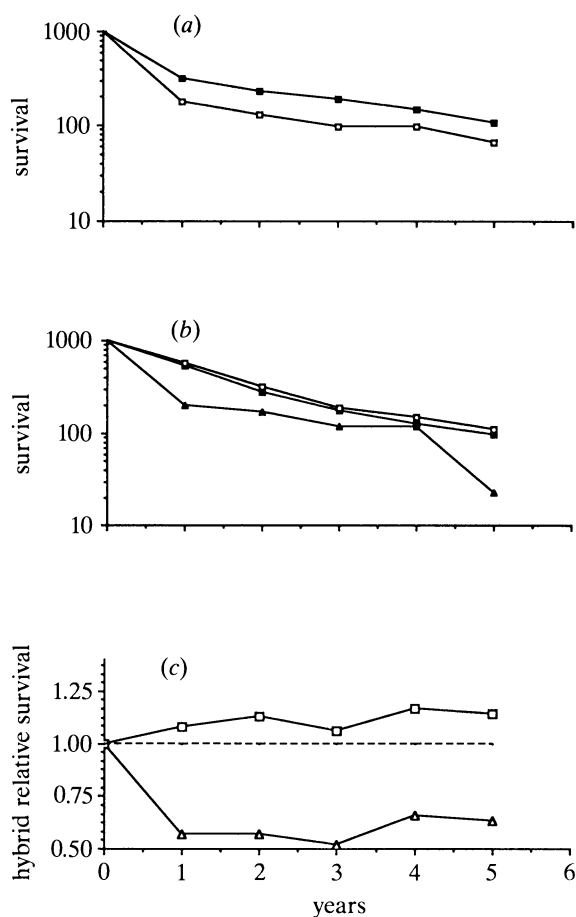


Figure 5. Survival; of *G. fortis*, *G. fuliginosa* and their F_1 hybrids before and after the El Niño event of 1982–1983. (a) The unweighted mean survival values for cohorts born in 1976, 1978, 1979 and 1981 for *G. fortis* (filled squares), hybrids (open squares) and *G. fuliginosa* (filled triangles). (b) The same for the 1983, 1984 and 1987 cohorts for *G. fortis* 1981 (filled squares), hybrids (open squares) and *G. fuliginosa* (filled triangles). Survival values weighted by sample sizes give the same patterns, differing only in small details. (c) Relative fitness expressed in terms of survival values of hybrids in relation to survival of *G. fortis* before (1976–1981 cohorts, open squares) and after (1983–1987 cohorts, open squares) the El Niño event. Relative fitness of hybrids was low before the event and high afterwards. Survival of hybrids of the first four cohorts was significantly lower than *G. fortis* survival by a χ^2 test (Lee 1980; Hutchings *et al.* 1991) applied to life-table data ($\chi^2_5 = 14.84$, $p < 0.025$). The difference in survival arose in the first year ($\chi^2_1 = 13.91$, $p < 0.001$), and was maintained unaltered thereafter. For the later cohorts there is no statistically detectable difference in survival ($p > 0.1$). Nevertheless, the small difference between hybrid and *G. fortis* survival is probably real, as almost the whole population of fledglings was included in the comparison; 97% of the 1983–1987 cohorts were ringed, whereas an estimated 80% of the 1976–1981 cohorts were ringed. Sample sizes are 957 *G. fortis*, 7 *G. fuliginosa* and 32 F_1 hybrids born in 1976–1981; and 2376 *G. fortis*, 25 *G. fuliginosa* and 68 F_1 hybrids born in 1983–1987.

Grant 1992*b*). Before 1983, *G. fortis* \times *G. fuliginosa* pairs produced a total of 32 fledglings. Only two survived to 1983, and none bred before that year. Hybrids born in 1983 and afterwards, however, had much higher fitness than those born before (figure 5). The lower panel of figure 5 expresses the survival component of fitness of

the F_1 hybrids in relation to the fitness (survival) of *G. fortis*. It shows that hybrids were at a strong disadvantage before the 1982–1983, El Niño event, and at a small advantage afterwards.

Hybrids bred during and after this event without showing signs of sterility or lower success than the parental species. Hybridizing pairs contributed more offspring (per pair) to the next generations than did non-hybridizing pairs because their offspring survived better. For example, by the end of the breeding season of 1991, *G. fortis* and *G. fuliginosa* individuals born in 1987 had not replaced themselves in terms of offspring fledged, but hybrids of these two species had more than replaced themselves by a factor of 1.3 (Grant & Grant 1992*b*).

The contrast between hybrid fitness before and after 1983 was even stronger for *G. fortis* \times *G. scandens* pairs. Before 1983 one pair produced one fledgling which survived for less than a year. In the breeding years 1983–1987 a total of five different pairs produced 23 fledglings. The F_1 hybrids born in 1983 and 1987 survived better than individuals from both parental species and *G. fortis* \times *G. fuliginosa* hybrids. Experiencing the same reproductive success as the other groups, they had the highest overall fitness as a result of their higher survival. Extensive backcrossing ensued (Grant & Grant 1992*b*).

The results show that hybridization is evolutionarily ineffective under some conditions and potent under others. A causal link with altered food conditions is likely. On average, F_1 hybrids are immediate in size between the hybridizing species sizes (G. R. Grant & P. R. Grant, unpublished observations), as is to be expected from the high heritabilities of morphological traits in *G. fortis* (Boag 1983). The two types of hybrids ($n = 9$ each) and *G. fortis* ($n = 72$) had higher proportions of small seeds in the diet than *G. scandens* ($n = 55$) in the period 1988–1991 (ANOVA, $F_{3,141} = 135.0$, $p < 0.001$; Student–Newman–Keuls post-hoc test, $p < 0.01$), but did not differ amongst themselves ($p > 0.1$). A fuller analysis is in preparation. Another obvious factor is genetic. The enhanced heterozygosity of hybrids might have conferred a general hybrid vigour. This factor would have been important if there had been a period of inbreeding (Gibbs & Gant 1989) and consequent loss of genetic variation before the successful outbreeding. Different, slightly deleterious, mutations might have accumulated in the different populations before they exchanged genes (A. S. Khondrashov, personal communication).

7. DISCUSSION

The evidence for selection for small beak size in the *G. fortis* population (lacking the hybrids) is consistent with the survival advantage experienced by hybrids at the same time. Although experimental verification is lacking, the two evolutionary changes were apparently caused by the common factor of a change in food supply. Moreover, the evolutionary response of the population to altered ecological conditions may have been facilitated by the large amount of additive genetic variation originating from earlier episodes of hybrid-

ization and backcrossing (Grant & Price 1981). Thus hybridization not only facilitates adaptation to extreme climate, as argued by Lewontin & Birch (1966), it can be enhanced by climatic extremes.

If unchecked by selection, hybridization should lead to fusion of the species into one population. The process has been modelled for *G. fortis* and *G. fuliginosa* (Boag & Grant 1984*b*). At the observed rate of interbreeding, no hybrid advantage and no selection, it would take more than 50 generations, or more than 200 years, to eliminate the morphological differences between them. The hybrid advantage documented for post-1983 years would reduce the duration to 100–200 years, and an increasing rate of interbreeding would reduce it further. Although we do not know how long the ecological effects of the 1982–1983 El Niño will persist, it seems unlikely they will last for that long. Climatic conditions on the Galápagos fluctuate on a timescale of decades or less (Grant 1985). When dry conditions similar to those before 1983 return, gene exchange should cease, hybrids produced before then should be at a disadvantage, and the three species will persist as three separate species, until the next extraordinary El Niño event occurs. Over the past 500 years, El Niño events classified as 'strong' have occurred one to three times per century (Quinn *et al.* 1987).

The preceding argument is contingent upon there being no net change in climatic conditions, only continuing and strong fluctuations. Global warming alters the argument. The phenomenon is widely accepted as real, although the causes are surrounded by conjecture and predictions about the future vary (Holt 1990; Lubchenko *et al.* 1991; Peters & Lovejoy 1992). Regardless of its magnitude, if global warming results in the more frequent occurrence of major El Niño events (Grant & Grant 1992*c*) then a return to pre-1983 conditions may not occur for many decades, perhaps a century, in which case the prospect of three species fusing into a single population becomes more likely.

The El Niño event of 1982–1983 had widespread effects on the Galápagos biota, destroying some elements of the vegetation while fostering the growth of others (Hamann 1985), altering the composition of marine algal communities (Glynn 1988), and decimating populations of marine iguanas (Laurie 1985), sea-lions and fur seals (Trillmich & Ono 1992), penguins and cormorants (Rosenberg *et al.* 1990), sea-urchins and corals (Glynn 1988, 1990). Effects were experienced in the tropical rainforests of Panama (Hubbell & Foster 1992) and Indonesia (Leighton & Wirawan 1986), and in seabird communities on Christmas Island (Schreiber & Schreiber 1984) and in Alaska (Percy & Schoener 1987). Natural selection may have occurred in many populations of animals and plants at that time, but few studies were in a position to detect it. The study on Daphne was one of only four in the Galápagos which used the same study methods on the same population(s) before and after 1983.

Small marine iguanas survived better than large ones at a time of heavy mortality in 1983 (Laurie 1990), whereas large land iguanas had a survival

advantage at that time (Snell 1987). Directional selection on beak size and shape was shown to occur in populations of *Geospiza conirostris* (large cactus finch) and *G. magnirostris* (large ground finch) on Genovesa island (Grant & Grant 1989). These species, and *G. difficilis*, also hybridize. As on Daphne, the fates of hybrids differed before and after 1983. However, unlike on Daphne, when small seed abundance declined after 1983, hybrids were at a disadvantage. The difference in relative fitness of hybrids on the two islands can be explained by the different food spectra (Grant & Grant 1989). None of those studies was able to assess the possibility of an evolutionary change taking place in response to directional selection.

The evolutionary change documented in the population of *G. fortis* on Daphne serves as a model for what has presumably happened countless times on a larger timescale in the past: small evolutionary changes in quantitative traits caused by natural selection under changing environmental conditions. The changes may be oscillating or unidirectional, influenced by hybridization or not, and result in enhanced (Genovesa) or reduced (Daphne) differences between closely related species. They have an important bearing on speciation, adaptation, the maintenance of genetic variation in populations, and the generation of biological diversity.

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