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Book Author(s): Peter R. Grant and B. Rosemary Grant

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# Competition and Character Displacement

No scientific theory is worth anything unless it enables us to predict something which is actually going on. Until that is done, theories are a mere game with words, and not such a good game as poetry.

(Haldane 1937, p. 7)

For empirical research, every island is a cause for celebration, a natural laboratory.

(Schalansky 2009, p. 17)

## Introduction

**C**OLONIZATION OF DAPHNE BY *MAGNIROSTRIS* had a profound effect on the community of finches, after a lag of 22 years. *G. magnirostris* apparently caused an evolutionary change in *fortis* morphology as a result of competing with it for food (character displacement; Grant and Grant 2006, Pfennig and Pfennig 2010, 2012). An evolutionary effect of competition in the present is the complement of character release, evolution of *fortis* morphology in the absence of competitors in the past (chapter 2). *G. magnirostris* is a potential competitor with the two resident species, especially *fortis*, because their diets overlap (fig. 6.11). The potential for competition could scarcely be realized in the first decade, when *magnirostris* numbers were so low (fig. 6.1), even though nonbreeders occasionally immigrated, reduced

the supply of large seeds to some extent (Boag and Grant 1984b), and might have had short-term effects on the *fortis* population. The potential was realized much later, during a severe drought.

The chapter is structured to show how a competitive influence of one species on another can take three forms: diets diverge in the food-limited dry season, mortality rates increase, and survival depends on phenotype. These competitive effects are respectively behavioral, ecological, and evolutionary. The first two are explored with *fortis* and *scandens*. Before the mid-1990s, at a time when *magnirostris* were scarce, population sizes of *fortis* and *scandens* were large enough that occasional competition between them could be expected in the dry season. Food availability varies among dry seasons as a result of strong interannual variation in seed production in preceding wet seasons (e.g., fig. 7.1). We investigated the possibility of competition by (1) comparing diets with food availability, and (2) examining mortality in relation to food availability and the numbers of potential competitors.

## Competition and Diet Overlap

Smith et al. (1978) suggested that if species competed for food, their diets would diverge as food supply declined from wet season to dry season. The predicted divergence was observed in a comparison of wet- and dry-season diets of different ground finch species on several islands in 1973, including *fortis* and *scandens* on Daphne. The comparison of dry-season diets was extended for another 12 years on Daphne (Boag and Grant 1984b, Grant and Grant 1996c), and the predicted divergence was observed in 10 of them, more frequently than expected by chance (Grant and Grant 1996b). The two exceptional years (and one other) were unusual in one respect that could justify their exclusion from the comparison. *Opuntia* flowers were abundant, and almost certainly this alleviated competition between the species because they were too numerous to be defended by *scandens*. The flowers are always an important component of the feeding niche of *scandens*, and important to *fortis* in proportion to their (flower) abundance.

## Effects of Competition on Survival

By depleting some parts of shared resources, one species could increase the mortality rate of another through starvation. If such a competitive process is going on, we expect a negative relationship between the numbers of a pair of interacting species (Gibbs and Grant 1987c,

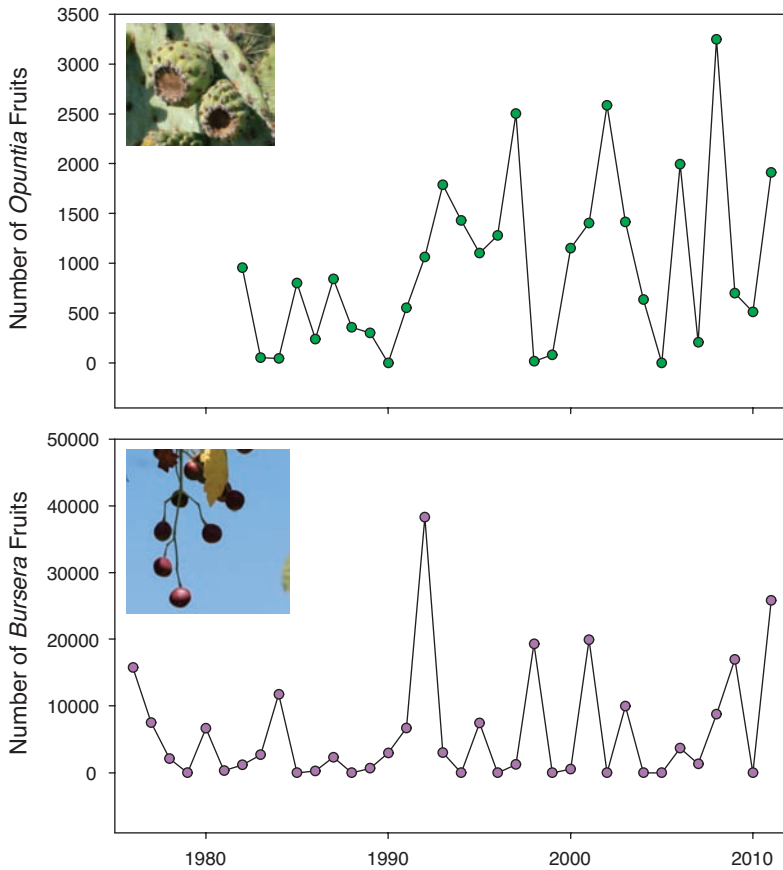


Fig. 7.1. Two indices of annual variation in plant reproduction: *Opuntia echios* (above) and *Bursera malacophylla* (below). Each year all fruits were counted on the same six *Opuntia* bushes on the plateau in or close to the first week of February, and all berries were counted or estimated on the same 79 *Bursera* trees on the plateau in years of production (21 others were males). Annual production is influenced by rain, but numbers of fruits or berries are not correlated with total rain in either *Opuntia* ( $r = 0.104$ ,  $p = 0.5837$ ,  $n = 29$ ) or *Bursera* ( $r = 0.182$ ,  $p = 0.2873$ ,  $n = 35$ ). Rain at the end of the dry season initiates flowering of *Bursera*, but heavy rain may destroy many flowers, as happened in the El Niño years of 1983 and 1987. Numbers of *Opuntia* fruits overestimate seed production in some years when alternative foods are scarce because *scandens* destroys the stigmas in reaching the pollen and nectar (fig. 2.17; Grant and Grant 1981); for example, almost all stigmas were destroyed in this way in 2004. Almost all *Bursera* berries are consumed in the first month after they mature, whereas *Opuntia* seeds and fruits remain available for the whole year. *Bursera* trees live for up to 200 years, extrapolated from a 25-year growth study of 100 trees (1976–2001) on the plateau. An *Opuntia* bush identified in a 1923 photograph (Beebe 1924) lived until 1989, for more than 66 years and an estimated minimum 80 years. Hamann (2001) estimated maximum life expectancies of 200 years for *Bursera* and 150 years for *Opuntia* from growth studies on three islands.

Grant and Grant 1996c): as one species becomes more common, the other becomes less common. For testing the competition hypothesis it is important to statistically control the influence of food supply on finch numbers because population sizes of *fortis* and *scandens* fluctuate together: high food production in some years and scarcity in others affect the two species similarly. When experimental control of food supply is not available for a test of competition (Martin and Martin 2001, Dhondt 2012), as here, statistical control is achieved by regression analysis. We regressed mortality of birds in their first year of life on abundance of small, medium, and large seeds, and on the number of adults of each of the species. Data were transformed appropriately (Grant and Grant 1996c).

Young birds of both species feed predominantly on small seeds in their first dry season because they are relatively common and easy to handle. Not surprisingly, therefore, first-year mortality of each species was found to vary negatively with the abundance of small seeds, and not with the abundance of medium and large ones (Grant and Grant 1996c). After the effects of small seeds were controlled statistically, the mortality of each species was found to vary positively with the abundance of adult *fortis* but not with the abundance of *scandens*. Small-seed abundance is more important (47.8% variance explained) than adult *fortis* numbers (18.7%) in determining survival of young *fortis*, whereas *fortis* numbers (38.9%) account for more of the variation in young *scandens* mortality than do small seeds (25.7%).

These results suggest a competitive asymmetry: intraspecific competition contributes to the mortality of young *fortis*, whereas interspecific competition with the more abundant *fortis* contributes to *scandens* mortality. Even though not demonstrated by the results, *scandens* probably does have some effects on juvenile *fortis* survival because they physically exclude them from feeding sites, especially *Opuntia* flowers and fruits.

Adult *fortis* mortality is influenced, like juveniles, by intraspecific and not interspecific competition. Their annual mortality is strongly predicted by their numbers. *G. scandens* adults are less dependent than the juveniles upon seeds, and their diet is dominated by various products of *Opuntia cactus* at which they, and especially the males, are socially dominant to *fortis*.

## Character Displacement

The third type of interspecific influence is evolutionary, causing a shift in phenotype in the next generation. Some phenotypes might be at a

selective disadvantage compared with others in the same population when competing with another species. Phenotypes best adapted at exploiting that part of the diet spectrum shared by another species would survive less well than the remainder of the population. The result would be character displacement, a shift in the phenotypic mean (Schluter 1994), and, to the extent that the phenotype is heritable, an evolutionary change in the next generation (Grant and Grant 2006).

*G. magnirostris* and *fortis* are potential competitors as a result of an overlap in their diets (figs. B.2.1 and 6.10), especially in the dry season (table 7.1 and fig. 6.11), when food supply is likely to limit population sizes (Grant 1986). The principal shared food is *Tribulus cistoides* (fig. 2.10). Seeds of this plant are contained within a hard mericarp and exposed when a finch cracks or tears away the woody outer covering (fig. 7.2). Only the large-beaked members of the *fortis* population are capable of removing seeds (chapter 4), and on average they take three times longer than *magnirostris* to gain a seed reward (Boag and Grant 1984a, Grant 1981b). *G. magnirostris* compete with *fortis* in two ways, by interference and by exploitation. They physically exclude them from *Tribulus* feeding sites, and they reduce the density of *Tribulus*

**TABLE 7.1**  
Proportions of seeds in the diets of three finch species

Species	Year	N	Small	Medium	Large
<i>G. fortis</i>	1977	216	0.731	0.102	0.167
	1985	205	0.805	0.000	0.195
	1989	628	0.771	0.051	0.162
	2004	97	0.804	0.113	0.082
<i>G. magnirostris</i>	1985	27	0.185	0.000	0.815
	1989	68	0.059	0.118	0.823
	2004	110	0.045	0.264	0.691
<i>G. scandens</i>	1977	115	0.852	0.148	0.000
	1985	96	0.771	0.219	0.000
	1989	145	0.234	0.697	0.000
	2004	98	0.174	0.826	0.000

*Note:* See also fig. 6.11. Small seeds are a composite group of 22 species, medium seeds are *Opuntia echios*, and large seeds are *Tribulus cistoides*. *N* is the number of observations. There is strong heterogeneity in the *fortis* feeding data ( $\chi^2_6 = 30.979$ ,  $p < 0.0001$ ). The reduction in *G. fortis* feeding on *Tribulus* in 2004 makes a significant contribution ( $\chi^2_1 = 3.912$ ,  $p < 0.05$ ). Data were obtained by observations in the first three months of each year. In 1977 (only), when *fortis* with large beaks had a selective advantage, the proportion of large seeds in the diet rose to 0.304 (June) and 0.294 (December). From Grant and Grant 2006.



Fig. 7.2 Character displacement. Large members of the Medium Ground Finch (*fortis*) population (A) died at a higher rate than small members (C) in 2004 owing to depletion by Large Ground Finches (*magnirostris*) (B) of the large and hard fruits of *Tribulus cistoides* (D). Five mericarps constitute a single fruit. The left-hand mericarp is intact. The right-hand mericarp, viewed from the other (mesial) side, has been exploited by a finch, exposing five locules from which seeds have been extracted. Mericarps are about 0.8 mm long. From Grant and Grant 2006.

fruits to the point at which they are probably no longer profitable for *fortis* to exploit, owing to handling inefficiencies in relation to search and metabolic costs (Schluter et al. 1985, Boag and Grant 1984a, Grant 1981b, Price 1987). Thus competition is mutual but not equal. By depleting the supply of *Tribulus* fruits, *magnirostris* is predicted to cause a selective shift in *fortis* in the direction of small beak size.

The predicted shift occurred 22 years after the founding of the *magnirostris* population (fig. 7.3; Grant and Grant 2006). By 2003 the combined numbers of residents and immigrants reached a maximum of  $354 \pm 47$  (s.e.). Scarcely any rain fell in 2003 (16 mm) or 2004 (25 mm), there was no breeding in either year, and numbers of both species declined drastically from 2004 to 2005. During the last phase of the decline *fortis* with large beaks were at a strong selective disadvantage, and the average beak size fell to an unprecedentedly low level

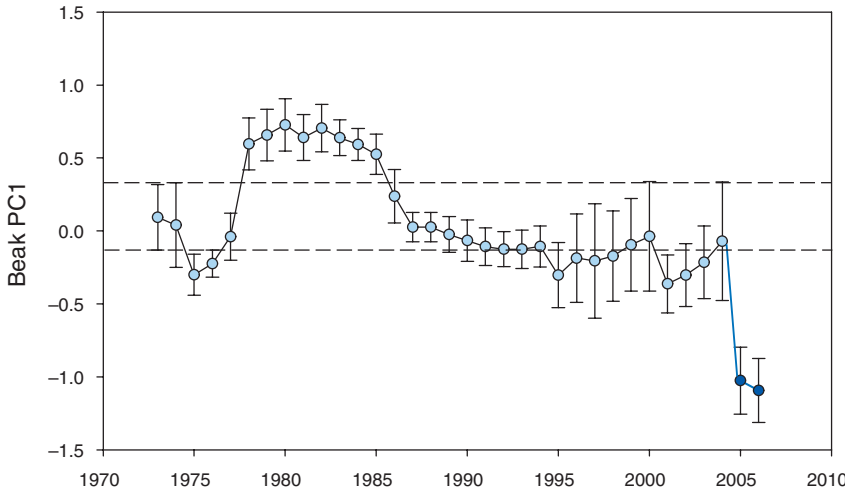


Fig. 7.3 Mean beak size (PC1-beak) of adult *fortis* (sexes combined) in the years 1973–2006. Vertical lines show 95% confidence intervals for the estimates of the mean. Horizontal, parallel dashed lines mark the 95% confidence limits on the estimate of the mean in 1973 to illustrate subsequent changes in the mean. Sample sizes vary from 29 (2005) to 950 (1987). The effect of strong selection in 2004 is highlighted in dark blue. Adapted from Grant and Grant 2006.

(fig. 7.3). Two factors that might have contributed to the selective advantage of *fortis* with large beaks in 1977–78—social dominance of large birds and the higher rate of heat dissipation without water loss from the base of large beaks (chapter 4) (Greenberg et al. 2012)—could not have contributed to selection in 2003–5, despite the same climatic conditions.

#### STRENGTH OF SELECTION

Coefficients of selection on *fortis* were uniformly large and negative, whether males and females were treated separately as in table 7.2 or combined. Average selection differentials for the six traits in standard deviation units (males 0.522, females 0.972) are unusually large compared with values reported in studies of other organisms (e.g., Hoekstra et al. 2001, Kingsolver et al. 2001, Kingsolver and Diamond 2011). All traits are strongly and positively correlated, so the question arises as to which, if any, was the most important factor that distinguishes survivors from nonsurvivors. To answer this we used principal components analysis to reduce the six intercorrelated traits to three independent



TABLE 7.2  
Standardized selection differentials (*s*) for *fortis* in the presence (2004) and absence (1977) of *magnirostris*

	2004		1977	
	Males	Females	Males	Females
Weight	−0.36	−0.93*	+0.88****	+0.90****
Wing length	−0.42	−0.69	+0.43***	+0.75***
Tarsus length	−0.44	0.23	+0.29	+0.22
Beak length	−0.78***	−1.50****	+0.73****	+0.76***
Beak depth	−0.49	−1.39****	+0.81****	+0.73***
Beak width	−0.54	−1.09***	+0.70****	+0.62*
PC1-body	−0.46	−0.79	+0.68****	+0.75***
PC1-beak	−0.64*	−1.39****	+0.79****	+0.74***
PC2-beak	−0.63*	−0.19	+0.20	+0.24
Overall mean	−0.55	−0.96	0.61	0.63
Sample size ( <i>n</i> )	49	23	171	58
Proportion surviving	0.41	0.61	0.47	0.45

Note: Statistical significance at  $p < 0.05$ ,  $< 0.01$ ,  $< 0.005$ , and  $< 0.001$  is indicated by \*, \*\*, \*\*\*, and \*\*\*\* respectively. Not included in the 1977 calculations are 135 birds of unknown sex (chapter 4; cf. tables 4.1 and 4.2); the sex was known for all birds in the 2004 sample. Despite the small proportion surviving (0.10), their selection differentials are almost identical (average 0.642) to an average of the male and female differentials. Also excluded were birds captured in 1978 (one) and 2006 (two) that may have been alive in 1977 and 2004 respectively but could have hatched later. Variances did not differ significantly between survivors and nonsurvivors in each selection event.

ones: body size, beak size, and beak shape. The answer is overall beak size; PC1-beak (beak size) was a strongly selected trait in females and in both sexes combined, whereas PC2-beak (beak shape) was not selected in males or when sexes were combined. Multiple regression analysis confirmed the primacy of beak size. Moreover there was little effect on body size, unlike the 1977 episode. In contrast to *fortis*, *magnirostris* experienced nonselective heavy mortality, although the small samples do not permit a sensitive test: 5 surviving males did not differ from 28 nonsurvivors in any of the six measured traits (all  $p > 0.1$ ), nor did the 2 surviving females of the 32 alive in 2004 (Grant and Grant 2006, with minor changes).

THE CAUSAL ROLE OF *G. MAGNIROSTRIS*

There are four reasons for believing that *magnirostris* played a causal role in the character displacement of *fortis*.

**HIGH IMPACT ON FOOD SUPPLY.** The potential impact of *magnirostris* was greatest at the beginning of 2004, when their numbers ( $150 \pm 19$ ) were closer to those of *fortis* ( $235 \pm 46$ ) than at any other time. Daily energy intake of the two populations and hence impact on the food supply was approximately the same at this time since *magnirostris* individuals ( $\sim 30$  g) are approximately twice as heavy as *fortis* ( $\sim 17$  g).

**SUPERIOR FEEDING EFFICIENCY ON SHARED COMPONENT OF THE DIET.** *G. magnirostris* are largely dependent on *Tribulus* seeds (fig. 6.11), which are depleted but not renewed during droughts. A much higher fraction of *magnirostris* than *fortis* feed on *Tribulus* (table 7.1), and they deplete the supply of seeds faster than *fortis*. We have calculated that seeds consumed by a *magnirostris* individual each day are sufficient for two *fortis* individuals to meet their energy needs if they feed on nothing else (Boag and Grant 1984a). As a result of their joint reduction in the number of seeds, *fortis* fed on *Tribulus* in 2004 only half as frequently as in other years (table 7.1). Feeding rates of *magnirostris* were exceptionally low, implying food scarcity. For example, in 2004 at least 90 individuals were observed foraging for *Tribulus* mericarps for 200–300 s, and none obtained seeds from more than two mericarps. Under the more typical conditions prevailing in the 1970s a total of eight birds observed for the same length of time fed on 9–22 mericarps, and the average interval between successive mericarps was only  $5.5 \pm 0.5$  s (s.e.) (Grant 1981b).

**PARALLEL DECLINE DUE TO STARVATION.** Numbers of *fortis* declined to a lower level in 2005, estimated by observations to be 83 (Grant and Grant 2006), than at any time since the study began in 1973. Numbers of *magnirostris* declined so strongly from the 2003 maximum through 2004 that by 2005 only 4 females and 9 males were left. The population was on the brink of extinction as a result of exhaustion of the standing crop of large seeds and starvation. Of 137 *magnirostris* that disappeared in 2004–5, 13.0% were found dead, and so were 21.7% of 152 *fortis*. They starved to death (fig. 7.4), as was evident from their empty crops and stomachs (23 *magnirostris* and 45 *fortis*). Absence of alternative large seeds was a contributing factor to the high mortality of both species. *Opuntia* cactus production in 2004 (fig. 7.1) was the fourth lowest since records were first kept systematically in 1982. Cac-

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Fig. 7.4 (*facing page*) Starvation during droughts. **Upper:** Dead *magnirostris*, skeletal, bands showing, 1990. **Middle:** *scandens* (above), *fortis*, and *magnirostris*, 2004. **Lower:** about 50 individuals of all species in 2004. Most were found in the small craterlet above the main crater illustrated in figures 1.4 and 1.5. From Grant and Grant 2008a.



tus seeds were insufficient for the two granivore species to escape the dilemma of a diminishing supply of their preferred foods, and insufficient for the cactus specialist *scandens* (~20 g). Their numbers, like those of *fortis*, fell lower (to 50) than in any of the preceding 32 years, without there being any connection between survival and beak size.

**KEY DIFFERENCE BETWEEN 1977 AND 2004.** In 1977, a year of only 24 mm of rain and no breeding, body size and beak size of both male and female *fortis* considered separately were subject to selection (table 7.2). Average selection differentials were 0.611 for males and 0.634 for females, and they were uniformly positive. In 2004, with the same amount of rain, selection differentials were similar in magnitude to those in 1977 but uniformly negative. Selection occurred in the intervening years (chapter 4), but the events of 1977 and 2004 stand out against a background of relative morphological stability (Grant and Grant 2002a) (fig. 7.3). Immediately prior to 2004 there was no unusual rainfall to cause a change in composition of the food supply or plant community, and no other unusual environmental factor such as temperature extremes or an invasion of predators such as owls or egrets, yet large finches survived at a low frequency in 2004 and at a high frequency in 1977. The conspicuous difference between these years was the number of *magnirostris*: 2–14 occasional visitors in 1977 (Boag and Grant 1984b), in contrast to  $150 \pm 19$  residents at the beginning of 2004.

#### EVOLUTION OF A DISPLACED CHARACTER

An evolutionary response to strong directional selection against large size is to be expected from the high heritability of beak size of *fortis* (Boag 1983, Grant and Grant 1995a, Keller et al. 2001). This was in fact observed. The mean beak size (PC1-beak) of the generation produced in 2005 and measured in 2006–08 was significantly smaller than the 2004 sample of the parental generation before selection ( $t_{184} = 4.55$ ,  $p < 0.0001$ ). The difference between generations is 0.65 standard deviations, which is exceptionally large (Kingsolver et al. 2001, Grant and Grant 2002a). It may be compared with the range of values predicted from the breeders' equation (Falconer and Mackay 1995, Lynch and Walsh 1998), namely, the product of the average selection differentials of the two sexes and the 95% confidence intervals of the heritability estimate. We used the heritability estimated from the father-offspring regression, having excluded offspring of extra-pair paternity (chapter 3), and thereby avoided inflation due to maternal effects of unknown magnitude. The observed value of 0.65 s.d. falls within the predicted



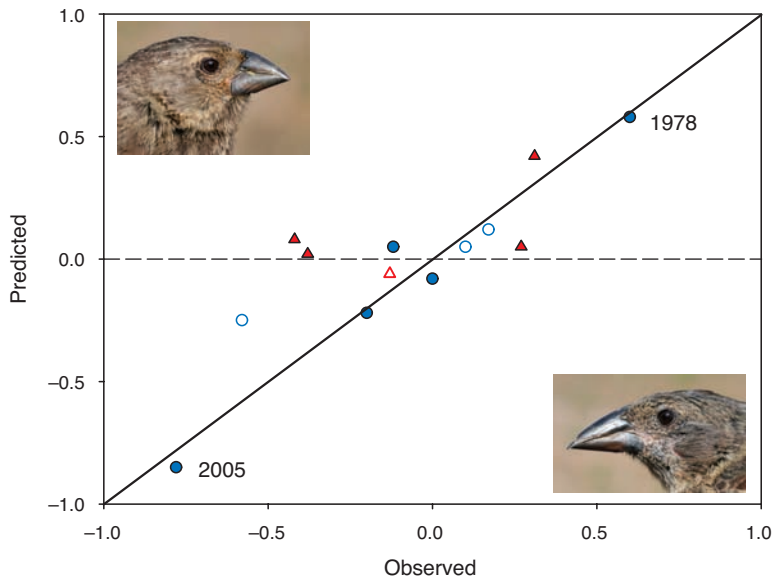


Fig. 7.5 Observed evolutionary responses to natural selection on beak size (filled symbols) and shape (open symbols) in *fortis* (circles) and in *scandens* (triangles) compared with predicted values. Note the response of *fortis* in 2005 is in the bottom left-hand corner. The reference line has a slope of 1.0: observed = predicted. Predictions are the product of the selection differential and heritability in standard deviation units at different times in the study. All selection differentials were significant at  $p < 0.01$ . Responses are positive for size increases and negative for decreases. Equations that take genetic correlations between traits into account (box 4.2) produce similar results because the correlations are all strong and positive (Grant and Grant 1994, 1995a).

range of 0.48–1.06 s.d. While a small component of the response is possibly attributable to environmental factors (Boag 1983, Grant and Grant 1995b; also chapter 4), the major component is genetic. There was plenty of food and low finch density after selection over the next few years, yet average beak size remained small, reflecting high heritability and no further selection. This was the strongest evolutionary change in the whole study (fig. 7.5).

#### G. *FORTIS* AND *SCANDENS* COMPARED

The difference in diet between *fortis* and *scandens* explains why *fortis* underwent evolutionary change in beak depth (fig. 1.6) whereas *scandens* did not (fig. 1.7). An ability to find and extract seeds of *Tribulus*

*cistoides* made the difference between survival and starvation in the *fortis* population at two times under contrasting conditions. *Tribulus* seeds are not in the *scandens* diet (fig. 6.11).

## Some Implications

We began by considering the absence of *fuliginosa* as a key factor in permitting an evolutionary shift of *fortis* to small size (chapter 2). We concluded that the particular food supply on Daphne and freedom from interspecific competition jointly explained why *fortis* were small: the hypothesis of character release was upheld. We now see that directional evolution of *fortis* in the past may have been partly driven by *magnirostris* and not just permitted by the absence of *fuliginosa*. From this we gain an insight into the early insular history of the Daphne finch community discussed in chapter 2. A possible reason why the *fuliginosa* population became extinct is that it suffered from competition with *fortis*, which were small as a result of competition with *magnirostris*.

Whether this speculation is correct or not, the evolutionary changes we observed are much more complex than those envisaged by Lack (1947), and by us. Composition of the food supply changes across years; so does the composition of the finch community. The average beak size of *fortis* does not occupy a fixed position on an adaptive landscape as implied by figure 2.16 but changes because the landscape, dominated by *Tribulus* seeds, is dynamic on a scale of years (fig. 7.6), and even months within years (fig. 4.5). The average beak size of *fortis* was closely aligned to the peak in the absence of a competitor, *magnirostris* (fig. 2.16). But as the present chapter shows, it was displaced from the peak by *magnirostris* to the left, toward smaller size, as predicted. The strong decline in *fortis* numbers further indicates a strong reduction in the height of the peak, although this was not measured. Recognizing the lack of constancy in an adaptive landscape such as this, Merrell (1994) has recommended “adaptive seascape” as a better term!

These observations have some interesting implications for evolution on Daphne on a scale longer than a few decades. *G. magnirostris* is likely to have been a resident breeder in the past, perhaps many times, and to have become extinct, perhaps many times, which implies a long-term, changing composition of the finch community and its evolutionary dynamics. The long-term evolution of *fortis* is therefore best viewed as determined by the presence or absence of two species of competitors and not just one: a seesaw dynamic of oscillation in eco-morphological

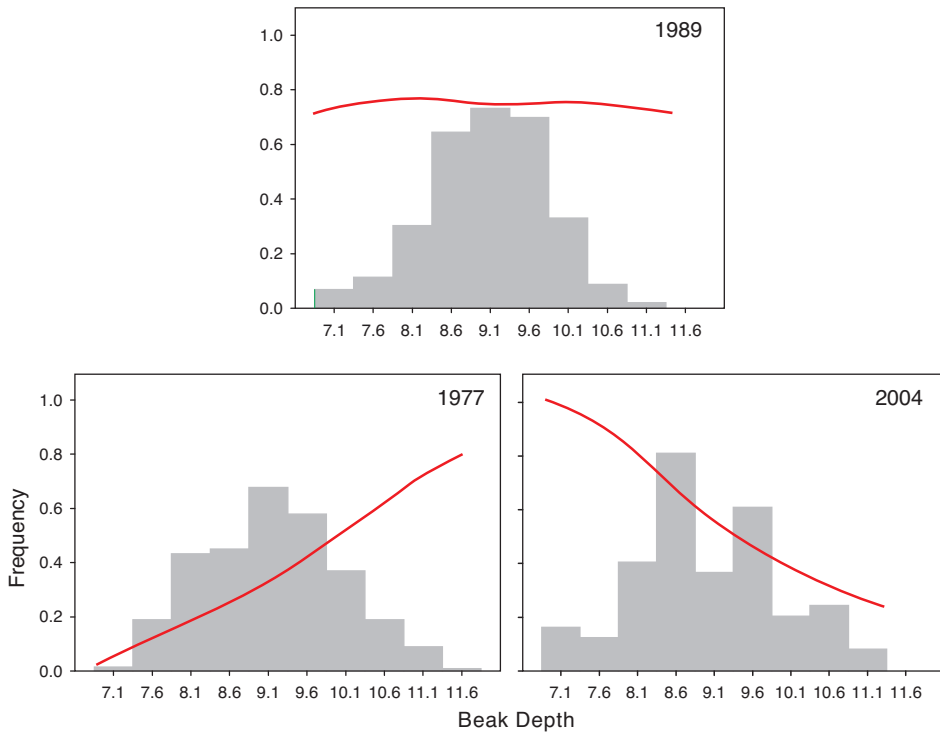


Fig. 7.6 *G. fortis* selection functions in three contrasting years. Selection functions are cubic splines (smoothing function 10) fitted to survival data. They are superimposed on beak-depth frequency distributions. Relative fitness does not vary significantly in most years; the 1989 sample ( $n = 554$ , omitting two outliers) is the largest.

space defined by reciprocal interactions with the other species and each other, and a changing food supply (fig. 7.6). The result is a nondirectional cycle of expansion and contraction of the community about the core central species, *fortis*, driven by competition, evolution, extinction, and reinvasion. In other systems, including island populations of lizards (Roughgarden 1995), cycles of changing community membership are directional through sequential replacement of one species by another that is larger or smaller.

A second implication follows from the long delay before character displacement occurred; it requires special circumstances. Those circumstances were an initially high density of consumers (finches) and a food supply that is strongly depleted and not replenished for many months, resulting in unusually heavy mortality of the consumers. Thus,

although the species were in potential competition at all times, there was in fact little or no competition, and no microevolutionary effects, until those special circumstances arose.

A third implication is that current morphology may reflect past evolutionary forces to some extent, as well as contemporary ones. After the rains of 2005 ended the two-year drought, the supply of *Tribulus* seeds quickly regenerated because *Tribulus* plants are perennial. *G. fortis* did not return to its pre-2005 morphological state of large size when *magnirostris* density stayed relatively low in 2006–8, but remained morphologically frozen in the new state of small size. There were no droughts, and dry-season survival was greater than 60%. The *fortis* population may have experienced stabilizing selection around a new optimum, but if so it was too weak to be detected, and we saw no signs of it in finch measurements. We prefer an alternative interpretation to stabilizing selection: no selection. *G. fortis* were small in 2012 because of selection in 2004–5 and not because of any selection in 2012. In 2008 the *magnirostris* population size rapidly rose to an unprecedented high level (fig. 6.1), so competition with *fortis* for large seeds may have resumed at that time.

## Summary

In this chapter we return to the question of competition raised in chapter 2. Species may compete for food, with behavioral, ecological, and evolutionary consequences. By studying populations for many years, we observed three kinds of competitive influences on *Daphne*: behavioral, ecological, and evolutionary. Diets of *fortis* and *scandens* overlap, and from wet season to dry season their diets diverge in most years, which is the expected consequence of competition. Survival of each species was assessed by multiple regression analysis of first-year survival in relation to seed supply and numbers of adults. Interspecific competition with the more abundant *fortis* contributes to *scandens* mortality, whereas mortality of young *fortis* is affected only by intraspecific competition. Competition with *magnirostris* caused an evolutionary change in *fortis*. This happened toward the end of a two-year drought (2003–5) as a result of their joint and severe depletion of the supply of *Tribulus* seeds. *G. fortis* with large beaks were at a strong selective disadvantage; average beak size of the population fell to an unprecedentedly low level, and remained there for the next few years because no further selection occurred. This is an example of character displacement. The observed evolutionary response to natural selection



was the strongest recorded in the study, and exceptionally strong in comparison with other organisms elsewhere. The long delay before character displacement occurred shows it requires special circumstances: large numbers of competitors and severe competition for food. *G. magnirostris* may have been an important influence on *fortis* morphology in the past, even if it underwent repeated cycles of colonization, numerical increases, decreases, and extinction. Therefore current morphology may be partly a reflection of past evolutionary forces as well as contemporary ones.