Daphne Finches: A Question of Size

If it is assumed that the various sizes and shapes of
bills amongst the Geospizae have been developed as
adaptation to differences in food habit, then it must
be shown that the different species of the genus
feed on different species of seeds.

(Snodgrass 1902, p. 381)

If these predictions and declarations are mistaken,
then the hypothesis must be discarded, or at least
modified. If, on the other hand, the predictions turn
out correct, then the hypothesis has stood up to trial,
and remains on probation as before.

(Medawar 1991, p. 232)

Introduction

ON FIRST ENTERING THE GALÁPAGOS ARCHIPELAGO, a natu-
ralist is struck by the distribution of closely related species of
finches. Populations of the same species differ on average in
body and beak size from island to island, whereas on any one island
sympatric species differ discretely from each other in these character-
istics. How did the morphological differences between species come
about? Two previous investigators confronted this question. Lack
(1947) laid stress on three factors—natural selection, diversification
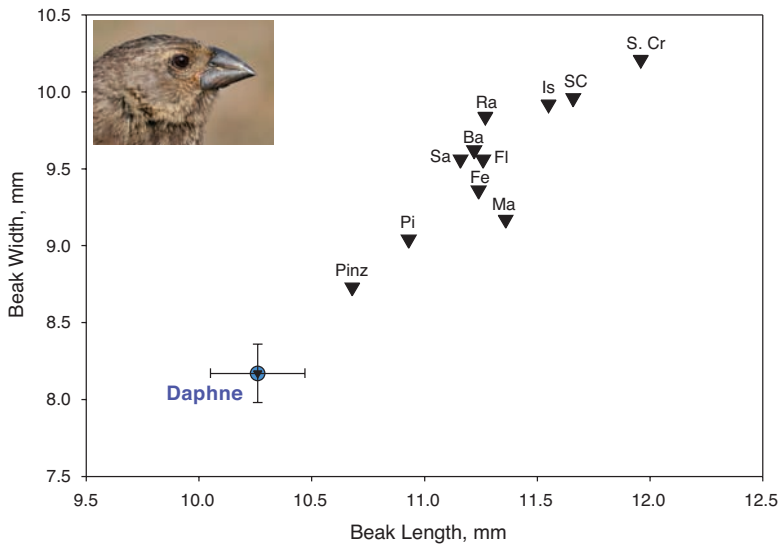on separate islands, and competition between species for food when

Fig. 2.1 Variation in average beak sizes among 12 populations of *fortis* (males), with 95% confidence intervals for the Daphne means. The Daphne samples are significantly smaller in both beak dimensions than all others including the most similar on Pinzón. Sample sizes vary from 11 (Rábida: Ra) to 278 (Floreana: Fl), with a median of 72. Other symbols refer to Balta (Ba), Fernandina (Fe), Isabela (Is), Marchena (Ma), Pinta (Pi), Pinzón (Pinz), Santiago (Sa), San Cristóbal (S. Cr), and Santa Cruz (SC). From data in Grant et al. 1985.

two closely related lineages came together on secondary contact (ch. 1)—whereas Bowman (1961) argued that available food on each island is sufficient to account for which particular species are present and their morphological characteristics, without having to invoke competition.

The focus of attention in this debate fell on Daphne, the reason being that on this island the Medium Ground Finch (*fortis*) is exceptionally small (fig. 2.1) and occurs there in the absence of the Small Ground Finch (*fuliginosa*). Elsewhere the Medium Ground Finch and Small Ground Finch coexist in the same habitat on 13 islands and differ substantially in size, but on the small island of Daphne the body size and beak size of *fortis* are intermediate between other members of its species elsewhere and *fuliginosa* (fig. 2.2). Lack explained the small size as character release, that is to say, expansion into the niche of an absent competitor, and hence the converse of character displacement described in chapter 1. Another situation strengthens the interpretation of character or competitive release. *G. fuliginosa* occurs alone on a group of four small islands called Los Hermanos (Crossmans) (figs. P.1
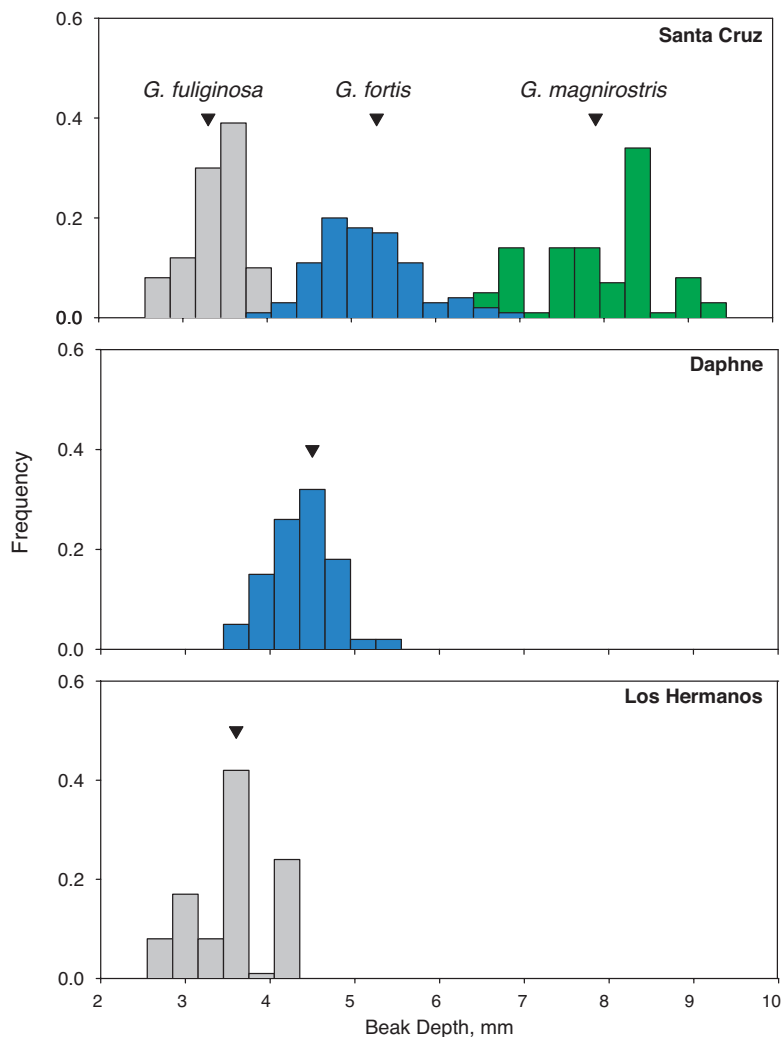
Fig. 2.2 Morphological intermediacy of solitary populations. Frequency distributions of beak depth (upper mandible) of adult males of three species of ground finches (*Geospiza*). Numbers of specimens: from Santa Cruz 134 *fuliginosa*, 156 *fortis*, and 26 *magnirostris*; from Daphne 89 *fortis*; and from Los Hermanos 12 *fuliginosa*. Solid triangles indicate average beak depths. From Grant 1986.

and 2.3), and here it is larger and intermediate in size between *fuliginosa* elsewhere and *fortis*. The two populations with intermediate body and beak sizes on Daphne and Los Hermanos are not identical; each is slightly more similar to the species to which it was assigned by Lack (1947).

Fig. 2.3 Seed sampling on other islands. **Upper**: Los Hermanos III. The study site is close to the top of the island. **Lower**: Ian and Lynette Abbott seed sampling at Bahía Borrero north shore of Santa Cruz.

For character release to be considered as the process resulting in the observed patterns, we need to know which is the original condition, on Santa Cruz or Daphne, and which is the derived one. In the case of *fortis* the allopatric state on Daphne is most likely to be the derived one. The island was once part of a large Santa Cruz–Baltra–Seymour Norte landmass in the last Ice Age (fig. 2.4), and only acquired its current island state about 15,000 years ago when the sea level rose (Grant and Grant 1996a, Geist et al. MS), probably abruptly (Blard et al. 2007). Thus *fortis*, in the absence of *fuliginosa*, could have been released from competition sometime after Daphne became an island. This has been described as the classical case of character release (Grant 1972, Boag and Grant 1984a).

David Lack made a convincing case for interspecific competition being an important factor in the evolution of Darwin's finches by concentrating exclusively on supporting evidence. However, observations elsewhere in the archipelago do not quite fit the pattern. For example, *fortis* is not intermediate in beak size on another small island (Champion) that lacks a population of *fuliginosa*. *G. fuliginosa* occurs in the
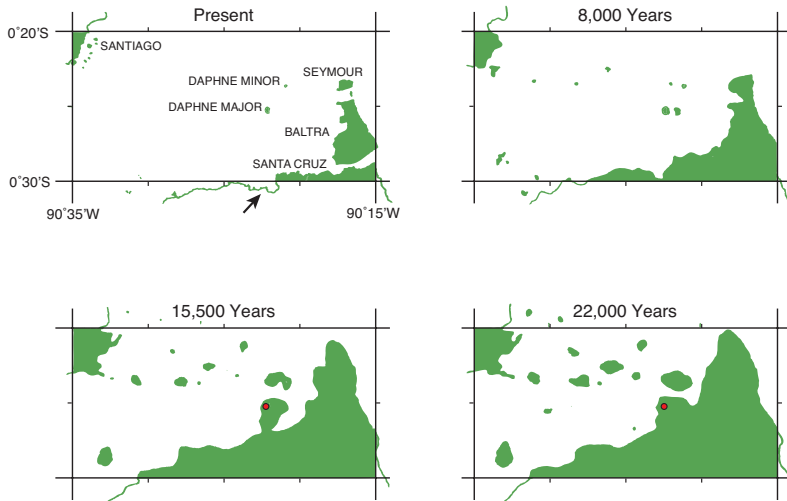
Fig. 2.4 Isolation of Daphne as a result of a rise in sea level associated with melting of glacial ice. From Grant and Grant 1996a, 2008a. The position of Borrero Bay is indicated by an arrow. The position of Daphne Major before 15,000 years ago is shown in red.

absence of *fortis* on eleven small islands and one large one (Española), yet has not become larger on any of them except on Los Hermanos. These facts raise doubts about the importance of competition.

Testing the Hypothesis

The character release hypothesis rests on five assumptions, which can be tested with *fortis* on Daphne. They are:

- Foods normally consumed by both *fortis* and *fuliginosa* are available on Daphne.
- Variation in diet is a regular function of variation in beak size. For seed-eating finches the obvious relationship is a mechanical or physical one: the average size of seeds in the diet increases as average beak-size increases among individuals.
- Natural selection is the process by which change takes place.
- There is heritable variation in the trait, or traits, that change.
- Finally *scandens*, the other finch species on Daphne, can be ignored because it contributes nothing to the morphological intermediacy of *fortis* by depleting resources.

Fig. 2.5 Map of Daphne, drawn from an aerial photograph. The study area used in 1973 for seed sampling, netting, and feeding observations is shown with a dotted-plus-solid line. This was extended in 1977 from the solid line to the outer slope. After 1978 the whole island was treated as the study area except for seed sampling. From Grant and Grant 1980a and Boag and Grant 1984a.

100m

Outer Slope

Inner

Plateau
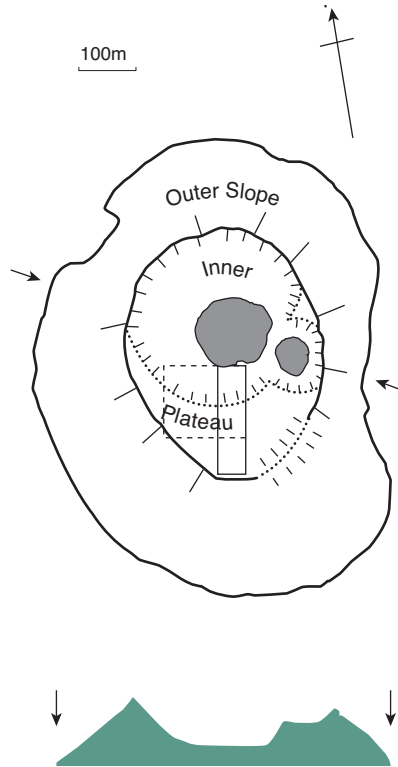
We test the first two and last assumptions in this chapter, the third assumption in chapter 4, and the fourth assumption in the next chapter.

AVAILABILITY OF FOOD

There was no published information on either food supply or diets on Daphne before we began. Testing the assumptions required a quantitative study of both. This was no simple task, because food supply depends strongly on rainfall, which varies markedly both within and between years (box 1.1). Quantifying available food required repeated sampling of seeds (box 2.1). We did this on Daphne (fig. 2.5) and, for comparison, at a coastal site (Borrero Bay, fig. 2.3) on neighboring Santa Cruz Island (fig. 2.4) at three times at the beginning of our study: April–May 1973, December 1973, and June–July 1975 (Abbott et al. 1977, Boag and Grant 1984a). The first and last samplings were in the early part of the dry season, rain and almost all seed production having ceased in the preceding three months, whereas the December sampling was at the end of the dry season when food is scarce.

DIETS OF *G. FORTIS* AND *G. FULIGINOSA*

Finches, like other birds, spend most of their lives searching for food and feeding. They eat seeds throughout the year and arthropods (caterpillars, aphids, etc.) predominantly in the wet season (fig. 2.6). To compare dry-season diets, we classified seeds by their size, measured as the second-longest dimension (depth, D), and hardness (H), mea-

Box 2.1. Estimating Food Supply

To quantify seed availability on Daphne, we established three sampling grids of 50 × 100 m on the inner slope, outer slope, and the plateau (slope 15°; figs. 1.4 and 2.5). On each sampling occasion we used a random-numbers table to select 50 1 m² quadrats distributed approximately equally among the three sampling grids (Abbott et al. 1977, Smith et al. 1978, Boag and Grant 1984a, 1984b). All buds, seeds, and fruits were counted on the vegetation. For counting seeds on the ground, we scooped out soil to a depth of ~2 cm in 25 × 25 cm areas in the northwest and northeast corners of each quadrat. We then multiplied the number of seeds on the ground and in the soil by 16 and added them to those on standing vegetation to give a total number per m². We sampled seeds twice per season each year and averaged them. We followed the same procedure on other islands (fig. 2.3) with only minor modifications and sampled on Santa Cruz only once per season each year.

To quantify diets we watched as many birds feeding as possible during mornings and, in the same areas, sampled food supply in afternoons of the same days. Initially finch diets were quantified by

Fig. B.2.1 Medium Ground Finches feeding. **Upper left**: Fruits of *Chamaesyce amplexicaulis*. **Upper right**: Capsules of *Sida salviifolia*. **Lower left**: Seeds and nectar of *Sesuvium edmonstonei*. **Lower right**: Spiderlings. From Grant and Grant 2008a.

Box 2.1. (continued)

recording identified foods eaten by a bird during a maximum of 300 seconds of observation (fig. 2.22). Then, in order to improve statistical analysis, we switched to recording just one food item per bird, the first item that could be identified, for as many birds as possible during morning hours. To compare quantitative features of the diets of *fortis* and *fuliginosa*, we classified seeds by their size, measured as the second-longest dimension (depth, *D*), and hardness (*H*), measured as the force needed to crack them (in kilogram force, kgf, then converted to newtons) in a specially constructed pliers device, the McGill seed cracker (fig. 2.7). A simple index $(D \times H)^{1/2} = (DH)^{1/2}$ was computed for each seed type (see appendix 1.1). Diets tell us what is meaningfully available to the finches. On Daphne finches consumed all seed types, from smallest to largest, except for two moderately large ones: *Merremia aegyptica* and *Ipomoea linearifolia* (appendix 1.1). They are both members of the Convolvulaceae and are possibly chemically protected, although doves eat both (Grant and Grant 1980a). They were deleted from our seed counts.

sured as the force needed to crack them (box 2.1, fig. 2.7), and then combined the two measures into the index $(DH)^{1/2}$. Our observations at the Santa Cruz site in the early dry season of 1973 showed that both species had broad diets (Abbott et al. 1977). *G. fuliginosa* fed on 13 different types of seeds and *fortis* fed on 11 types. At this time their diets were similar. On a scale of 0 to 1 the Whittaker similarity index was 0.87, as calculated by first determining the proportion (*P*) of each seed type (*i*) in the diet of each of the two species 1 and 2, and then summing the lowest values for all seed types: Σ min (P_{1i}, P_{2i}) (Whittaker 1960). Dietary differences were small but important. More *fuliginosa* fed on small and soft seeds than *fortis*, whereas only *fortis* fed on the largest and hardest seeds at this site, those of *Bursera graveolens* (fig. 2.8). Arthropods were absent from the diets at this time.

At the end of the dry season the dietary difference was more pronounced (Smith et al. 1978). A small number of temporary immigrants

Fig. 2.7 (*facing page*) Banding birds and measuring seeds. **Left**: Equipment for banding birds. **Right**: McGill seed cracker for determining the force necessary to crack a seed (Abbott et al. 1977). Finches can remove a split-ring band because the lower mandible is the same shape as the spoon used to apply the band to a leg. We changed from celluloid to plastic bands, applied by pliers. Colors are coded to correspond to numbers (box 2.2).

Fig. 2.6 Food for young finches. **Upper left**: Caterpillar on *Chloris virgata*. **Upper middle**: Caterpillar on *Sida salviifolia* (G. C. Keys). **Upper right**: Pair of sphingid caterpillar (*Hyles lineatus*?). **Upper middle left**: *Manduca* (?). **Lower middle left**: Caterpillar with warning coloration. **Middle center**: Green *sphingid* caterpillar. **Middle right**: Green *sphingid*. **Lower left**: Diptera larvae in *Opuntia* pad.
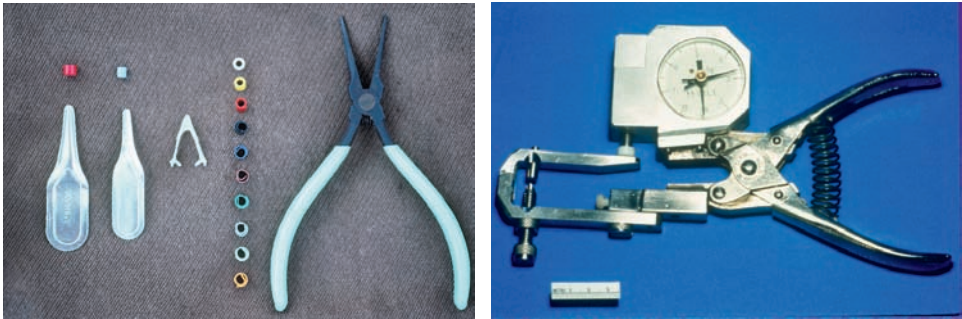
Fig. 2.8 Two important foods for finches. **Left**: *Bursera* berries. **Right:** *Croton* fruits. All finches are able to feed on the fleshy aril of *Bursera* berries, but only large-beaked birds can crack the woody stones and extract the kernels. *Croton* fruits are relatively easy to crack open (appendix 1.1).

- Tribulus
- Opuntia flowers
- Small seeds on ground
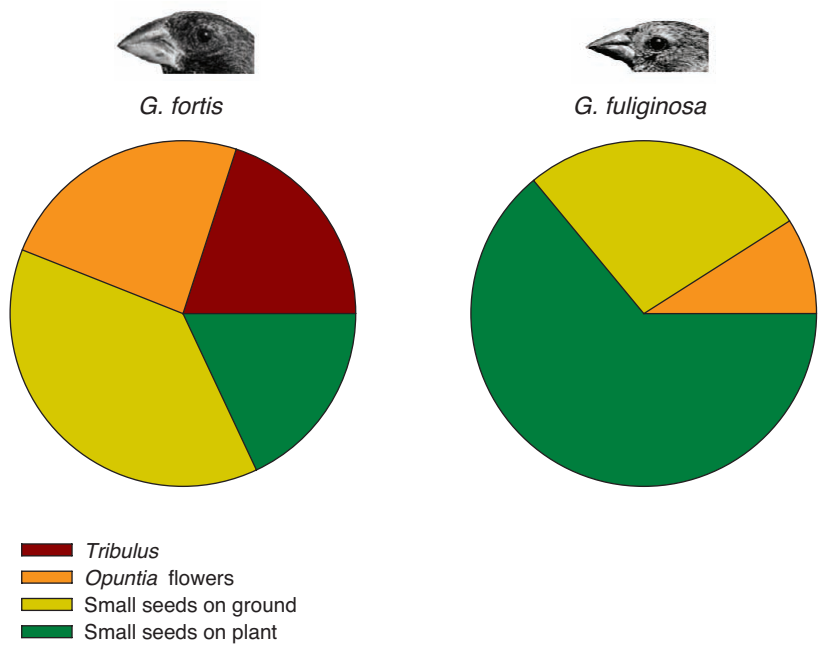- Small seeds on plant

Fig. 2.9 Diets of *fuliginosa* (*n* = 11 birds) and *fortis* (*n* = 66) at the end of the dry season on Daphne in 1973. The small seeds on plants comprise *Chamaesyce*, *Tiquilia*, and *Heliotropium* (appendix 1.1). From Boag and Grant 1984a.

Fig. 2.10 *Tribulus cistoides*. **Upper**: Flowering plant. **Lower**: Fruits. When mature and on the ground, the fruits are hard for finches to crack open. From Grant and Grant 2008a.

(*fuliginosa*) to Daphne allowed us to compare their diets with the diets of *fortis* there. As on Santa Cruz both species fed on the smallest and softest seeds (fig. 2.9), but only *fortis* fed on the large and hard seeds of *Tribulus cistoides* (fig. 2.10) with a depth-hardness index of approximately 10 (appendix 1.1). The difference between species in consumption of small and large seeds was also observed on Santa Cruz, and has been sustained in all subsequent studies on Daphne, Santa Cruz, and other islands, regardless of the particular identity of the large seeds (Grant 1986).

DIFFERENCES IN SEED SUPPLY

To test the first assumption, that foods normally consumed by both *fortis* and *fuliginosa* on large islands such as Santa Cruz are present on Daphne, we compared profiles of seed abundances of different sizes on Daphne and on neighboring Santa Cruz Island (Boag and Grant 1984a). Small seeds of grasses and other herbs eaten by *fuliginosa* on Santa Cruz are certainly present on Daphne. When the data are expressed in terms of total volume per seed size-hardness category, they show a relative paucity of the smallest seed classes on Daphne compared with Santa Cruz in the early dry season (fig. 2.11), but not in the late dry season. At the latter time Daphne had a larger volume of small-soft seeds than Santa Cruz (fig. 2.11). Furthermore at all three sampling times the largest and hardest seeds (*Tribulus cistoides*) were on Daphne.

These observations show, first, *fuliginosa* is not absent because its normal foods are absent, and second, *fortis* has not become small on Daphne as a result of large seeds being absent. These findings are consistent with the first assumption.
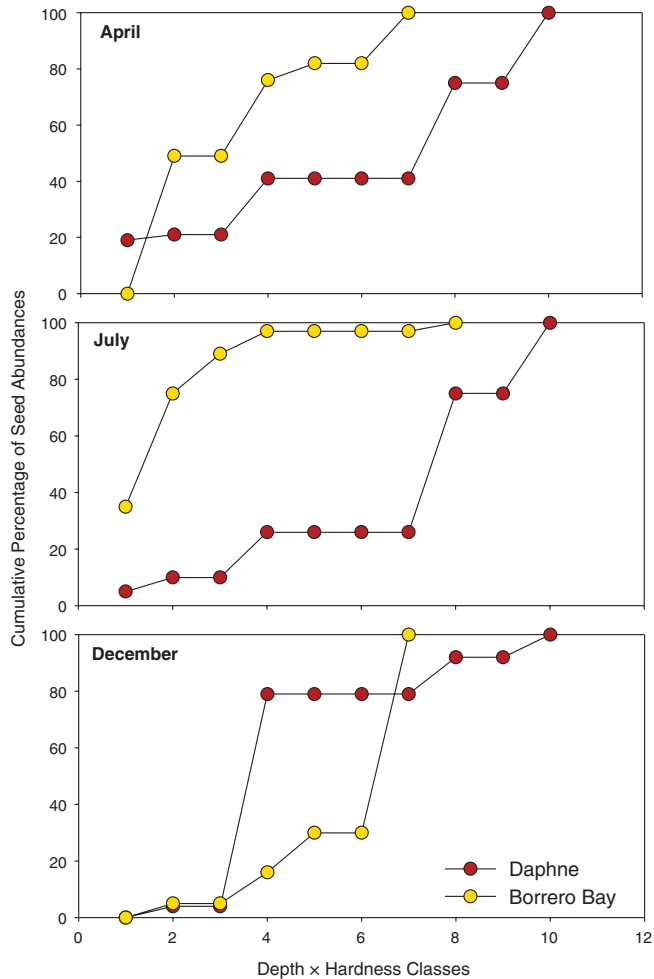
Fig. 2.11 Food distribution profiles in April and December 1973 and July 1975. Hardness classes are the square root of the product of seed depth and hardness (box 2.1). From Boag and Grant 1984a.

G. FULIGINOSA ON LOS HERMANOS

Feeding observations on Los Hermanos (fig. 2.3) give additional support to the hypothesis of character release. Late dry-season seed profiles are similar on Los Hermanos and Daphne in two respects: a scarcity of small seeds and prevalence of moderately hard seeds of *Cenchrus platyacanthus* (fig. 2.12) and even harder seeds of *Tribulus cistoides* (fig. 2.10). *G. fuliginosa* feed on both ripe and unripe seeds

Fig. 2.12 Plants that produce small seeds. **Upper left**: *Chloris virgata*. **Upper right**: *Eragrostis cilianensis*. **Middle left**: *Heliotropium angiospermum*. **Middle right**: Outer slope covered by *Portulaca howelli*. **Lower left**: Immature fruits of *Cenchrus platyacanthus*. **Lower right**: Mature fruits of *Cenchrus platyacanthus*. Small finches can open the soft immature fruits of *Cenchrus* but not the hard mature ones. Upper four figures are from Grant and Grant 2008a.

of *Cenchrus platyacanthus*, as *fortis* do elsewhere, whereas on other islands such as neighboring Isabela *fuliginosa* feed only on the soft, green, and immature seeds (Abbott et al. 1977, Boag and Grant 1984a, and fig. 2.12). Thus *fuliginosa* on Los Hermanos, in the absence of

fortis, are convergently similar to *fortis* on Daphne in diet as well as in morphology.

Association between Beak Size and Diet

The second assumption is that diet varies as a function of beak size. It is supported by numerous observations of seeds eaten by banded birds of known beak size. Very small seeds are picked up and consumed whole. All others are husked or cracked before the kernels are extracted and eaten. The force applied to the seed is a function of beak size, especially in depth and width dimensions, and muscle mass (Bowman 1961, Herrel et al. 2005, 2009). Therefore average seed size in the diet is expected to increase as average beak-size increases among individuals. This is indeed so at the level of species: *fortis* crack larger and harder seeds than *fuliginosa*. It is also correct at the level of individuals within the *fortis* population on Daphne (Grant et al. 1976, Grant 1981b, Price 1987) and on Santa Cruz (De León et al. 2011). In 1973–78 we captured, banded, and measured beak dimensions (in mm) of many birds (box 2.2, figs. 2.7, 2.13, and 2.14), and later recorded what they ate (Boag and Grant 1984a, 1984b). Those that fed on the largest and hardest seeds had much deeper beaks on average (9.95 ± 0.08 standard error; $n = 82$) than those that fed only on the smallest-soft seeds (9.28 ± 0.06; $n = 199$) (fig. 2.15). Birds that fed on seeds of medium size-hardness values but never on the largest-hard seeds had an intermediate average beak depth (9.73 ± 0.12; $n = 39$). Since males are larger than females, on average, this could simply reflect a sex difference in diets, but this is not the case. The difference in average beak size among the three dietary categories was found separately in a sample of males and females. In a detailed follow-up study Price (1987) confirmed that large individuals tend to forage more on large seeds than small individuals do, they consume large seeds more rapidly than smaller individuals do, and the smallest individuals do not feed on large seeds at all.

Adaptive Landscapes

Given the relationship between beak size and seed size, average beak size of each species on an island can be predicted from the food supply under the contrasting conditions of competition and no competition.
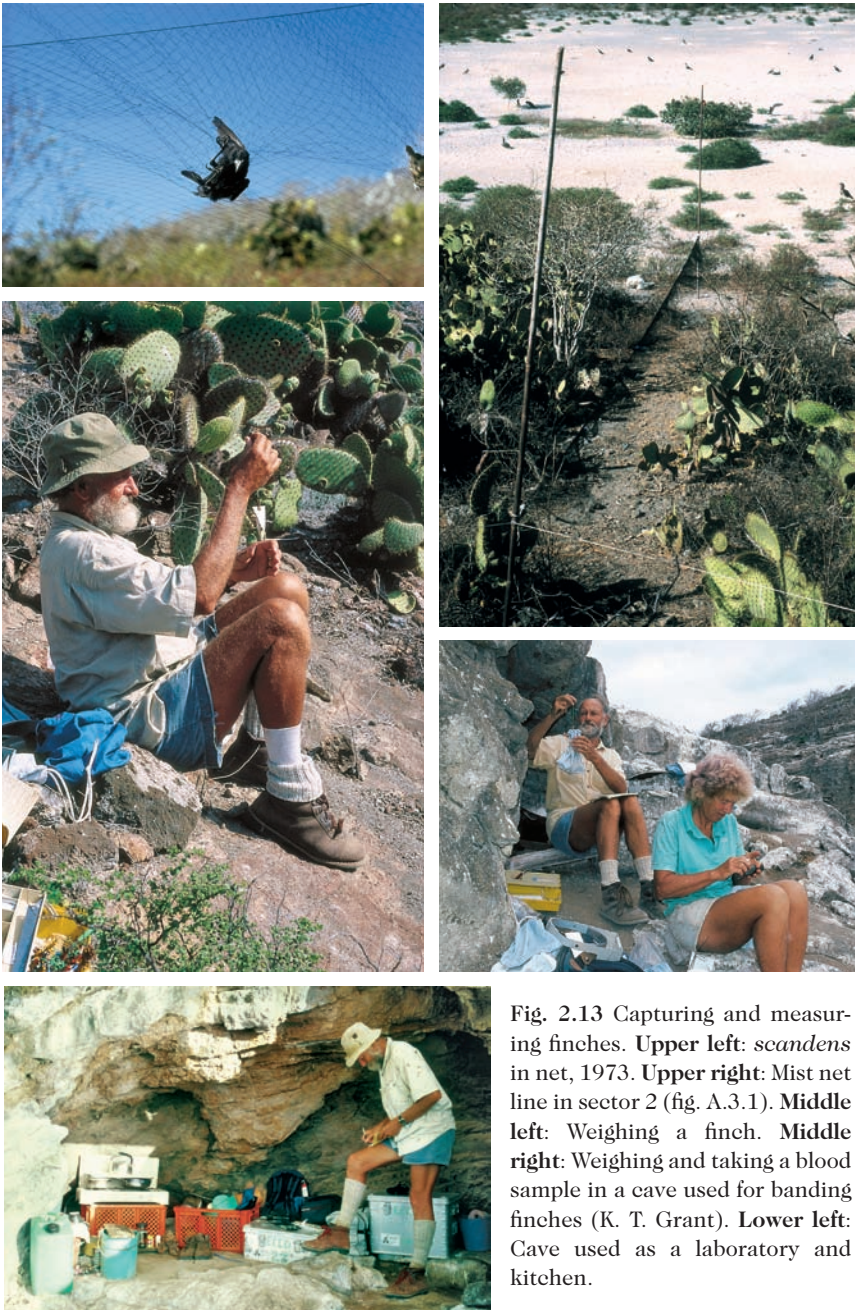
Fig. 2.13 Capturing and measuring finches. **Upper left**: *scandens* in net, 1973. **Upper right**: Mist net line in sector 2 (fig. A.3.1). **Middle left**: Weighing a finch. **Middle right**: Weighing and taking a blood sample in a cave used for banding finches (K. T. Grant). **Lower left**: Cave used as a laboratory and kitchen.

Fig. 2.14 Measuring a finch. **Upper left**: Beak length. **Upper right**: Beak depth. **Lower left**: Beak width. **Lower right**: Tarsus length. From Grant and Grant (2008a). Illustrated with a large cactus finch on Genovesa. The same measurements are taken on Daphne finches.
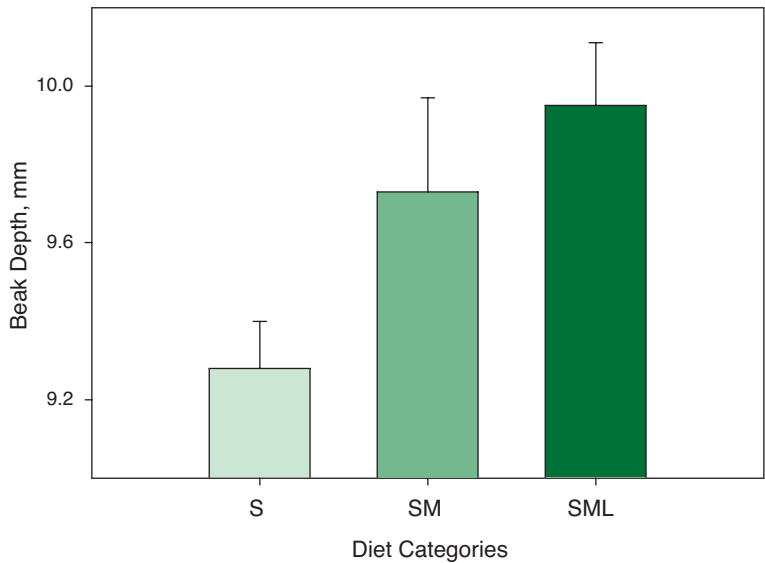

Fig. 2.15 Mean beak depths of *fortis* observed feeding on small seeds only (S), small and medium seeds (SM), or seeds of all sizes (SML). Lines represent 95% confidence intervals.

Box 2.2 Measuring and Marking Finches

For comparing diets with morphological features of individually marked birds, we captured finches in mist nets and measured and marked them with unique combinations of bands prior to release (figs. 2.7, 2.13, and 2.14). In the early part of the study we used mist nets mainly on the inner slope and plateau (Abbott et al. 1977, Smith et al. 1978, Boag and Grant 1984a). We measured six traits; four are illustrated in figure 2.14. We weighed birds to the nearest 0.1 g and measured wing length to the nearest mm with a wing ruler from the carpal joint to the wing tip, with feathers flattened and straightened. All other traits were measured to the nearest 0.1 mm (illustrated in Grant and Grant 2008a). Tarsus length was measured with dividers from the tarsometatarsal joint to the middle of the lowest undivided scute. Beak length was measured with dividers from the anterior edge of a nostril (nares) to the beak tip. Beak depth was measured with calipers in the plane of the anterior nares at right angles to the commissure, the line at which upper and lower mandibles meet. Beak width was also measured with calipers at the base of the lower mandible at the edge of the feathers. Later, when assistants measured birds, we applied correction factors to make their measurements comparable to ours.

Before releasing the finches, we marked them with unique combinations of leg bands for later identification. We used a numbered metal band (ring) and one colored band on one of the legs and two colored bands on the other leg. Colors were coded to correspond to the number (fig. 2.7). Starting alphabetically, we gave the number 0 to a black band, and so on with different colors for 1, 2, 3, etc, finishing with 9 for yellow. Bands were read in the sequence upper left leg, lower left, upper right, and lower right. Thus metal over yellow on the left leg and white over black on the right leg signified 980. To aid in identification, the metal band was placed in the upper position on either leg of *fortis,* and in the lower position on a leg of *scandens* or *fuliginosa.* We started by using celluloid bands (fig. 2.7). These were easily removed by the finches, and even when they weren't they became brittle and fell off. We switched to using split plastic (PVC) bands, first purchased commercially and then made by ourselves. These were much more successful, but some were not finch-proof. Gluing the split ends proved to be ineffective, therefore we made overlapping bands. We used thicker plastic bands for *magnirostris.*

Fig. 2.16 Predictions of average beak size compared with observations on a one-dimensional adaptive landscape. Histograms of beak depth are for *fuliginosa* (lined) and *fortis* (solid gray) adult males. Arrows pointing up indicate mean beak depths predicted by the food-based expected population density curves (the landscape topography), and arrows pointing down indicate the observed mean beak depths for *fuliginosa* (white) and *fortis* (gray). Adaptive landscapes are usually constructed in three dimensions (Svensson and Calsbeek 2012), but in this case nothing is gained by adding a third dimension such as beak length. From Schluter et al. (1985).
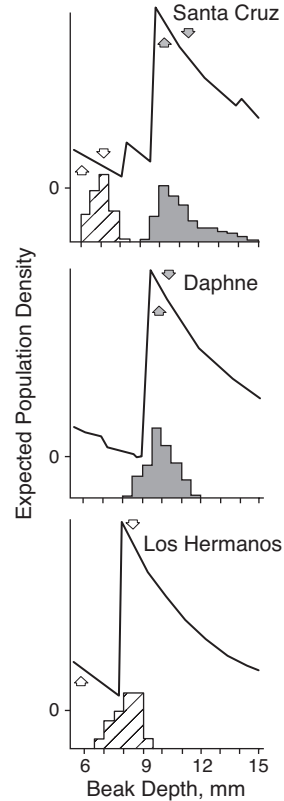
We addressed this task by using seed sampling data from the dry season, finch numbers, and beak sizes on many islands (Schluter and Grant 1984, Schluter et al. 1985). Density curves for a hypothetical solitary population were constructed as a function of average beak size for each island. This involved determining the range of seed sizes available for many populations of ground finch species with known mean beak depths, the density of seeds available within that range, and the number of finches supportable by the seeds. The procedure was repeated for 0.05 mm increments of beak depth across the whole size axis. The curves generated by the procedure can be considered as an adaptive landscape (Svensson and Calsbeek 2012) with peaks and valleys in fitness, unmodified by competition. Peaks and valleys are pronounced (fig. 2.16). Finally the species on each island were placed on the curves at the position(s) of their average beak sizes.

On Daphne there is no competition, and so the average beak size of *fortis* should be closely aligned to the average beak size predicted by the food supply, whereas in the competitive environment of Santa Cruz average beak sizes of *fortis* and *fuliginosa* should be displaced from their expected positions (fig. 2.16). This is what we observe.

On Los Hermanos *fuliginosa* shows an intriguing shift from the normal peak for that species to a second peak that is "occupied" elsewhere by *fortis*. As mentioned above, they consume the moderately large and hard mature seeds of a grass, *Cenchrus platyacanthus* (fig. 2.12), which elsewhere are consumed by *fortis*.

Can *G. scandens* Be Ignored?

The final ecological assumption is that *scandens*, the other finch species on Daphne, can be ignored because it contributes nothing to an explanation of the morphological intermediacy of *fortis*. When we first visited the island we discovered to our surprise that *scandens*, far from being scarce (box 1.3), was quite common. Therefore competition for food with *scandens* is a possible explanation for the relatively small beak size of *fortis* on Daphne. This hypothesis would be supported if *scandens* consumed seeds in the upper size range commonly exploited by the larger members of the *fortis* population on Daphne or other islands. Although *scandens* feed extensively on the seeds of the prickly pear cactus *Opuntia echios* ($DH^{1/2} \approx 3$) (figs. 2.17–2.20), and take a shorter time to crack them open than *fortis* (Grant and Grant 1996b), they do not open the harder, cherry-like, stones of *Bursera mala-*

Fig. 2.17 Exploitation of *Opuntia* cactus flowers. **Upper**: Some pollen has been consumed, but the central style and stigmas remain intact. **Lower**: A finch has removed the stigmas from this flower.

Fig. 2.18 Cactus fruits exploited by Cactus Finches. **Upper**: Opened *Opuntia* fruit on ground; seeds with green arils have been removed and consumed. **Lower**: *Opuntia* seeds have been cracked open, kernels removed, and then discarded. Lower figure from Grant and Grant 2008a.

Fig. 2.19 Cactus feeding. **Upper**: *scandens* pecking at *Opuntia* flower pollen. **Middle**: *scandens* probing an *Opuntia* flower for the basal nectar. **Lower**: *fortis* at an *Opuntia* flower that has been opened by *scandens* and half destroyed.

Fig. 2.20 Cactus seed eating. Cactus Finch cracking an *Opuntia* seed (L. F. Keller).

cophylla (fig. 2.8), nor do they feed on the harder woody fruits of *Tribulus cistoides* (fig. 2.10), unlike *fortis* (Grant et al. 1976, Grant 1981b). In view of dietary overlap *scandens* should not be ignored as a competitive influence on *fortis*, but the morphological shift of *fortis* to intermediate size cannot be attributed to *scandens* depleting the supply of large-hard seeds. The only other granivores on Daphne are doves (fig. 2.21). They may also exert competitive influences on finches, but have been ignored because they feed mainly on the two seed types not eaten by finches (box 2.1), and are generally rare (<20). They occur on all islands (Harris 1973).

Why Is *G. fuliginosa* Absent?

We presume that when Daphne was formed about 15,000 years ago, both *fortis* and *fuliginosa* were present, as they are today on the north shore of Santa Cruz. Subsequently one species became extinct on Daphne: why was it *fuliginosa*? If both species were equally vulnerable to becoming extinct it might have been a matter of chance which particular species did in fact become extinct. Alternatively, *fuliginosa*

Fig. 2.21 Other bird species. **Upper left:** Dove, *Zenaida galapagoensis*. **Upper right:** Yellow Warbler, *Dendroica petechia*. **Lower left**: Galápagos Flycatcher, *Myiarchus magnirostris* (K. T. Grant). **Lower right:** Galápagos Cuckoo, *Coccyyzus melacorhypha* (K. T. Grant). All eat insects, but only doves eat seeds. Doves and warblers are resident, and so are Galápagos Martins (*Progne modesta*), whereas flycatchers and cuckoos are occasional visitors to Daphne, especially after wet years of extensive breeding.

may have been competitively excluded by *fortis*. There is evidence for competitive exclusion in that only one species of granivorous finch is associated with an adaptive peak on all the 15 islands that have been studied. This implies a competitive adjustment of number of species on an island to the number of adaptive peaks (Schluter and Grant 1984). We suggest the reason why *fortis* prevailed on Daphne is that

the current peak in the adaptive landscape is closer to the peaks occupied by *fortis* on other islands than to peaks occupied by *fuliginosa* (Schluter and Grant 1984). Extinction of *fuliginosa* rather than *fortis* was therefore not just a matter of chance. The full range of seed sizes on Daphne is now exploited by the *fortis* population but not by *fuliginosa*. In a climatically fluctuating environment with interannual fluctuations in food supply (chapter 4) this puts the small *fuliginosa* at a long-term competitive disadvantage with the larger and more aggressive *fortis* and helps to explain why small numbers of occasional immigrant *fuliginosa* have not established a permanent breeding population.

Discussion

Speciation happened in the past, and we ask how did it happen? This is a historical question, and in the absence of fossils an answer has to be sought with living organisms by looking backward in time: a retrospective analysis. The usual technique is to compare populations at different stages on the way to becoming species, or even closely related species themselves, and to infer the causes of divergence in genetic or phenotypic characters that has already taken place (Coyne and Orr 2004). We adopted the different procedure of using information on contemporary populations to test assumptions of a historical hypothesis, the character release hypothesis of Lack. The conclusion from the tests, in the words of Medawar (1991), is that "the hypothesis has stood up to trial, and remains on 'probation' as before."

For the remainder of the book our approach is prospective. Studying populations through time provides insights into the process of speciation even if the progress toward complete reproductive isolation is small. It provides evidence of evolution, as illustrated in figure 1.6, and also allows us to identify environmental factors that cause it. In addressing the questions raised in chapter 1 we will revisit the competition hypothesis on probation in chapter 7, where we document character displacement in action. In the next chapter we discuss the heritable variation of size traits.

Summary

We chose to study Darwin's finches on the single island of Daphne because of an interesting morphological pattern discovered by David

Lack (1945). The Medium Ground Finch (*Geospiza fortis*) and Small Ground Finch (*G. fuliginosa*) are morphologically distinct where they occur together in the same habitat on 13 islands, whereas *fortis* occupies Daphne in the virtual absence of *fuliginosa* and here it is distinctly smaller, intermediate in body size and beak size between other members of its species elsewhere and *fuliginosa*. David Lack interpreted the pattern as evidence for interspecific competition causing divergence of the two species where they occur together, character displacement, and a release from competition when one species occurs alone. We use quantified information on food availability and diets to test three assumptions of the character release hypothesis, and find support for each. As assumed, food is available for both species on Daphne, beak size influences what size of seeds can be consumed, and a third species, *scandens*, can be ignored as a competitor for large and hard seeds. The evidence from Daphne indirectly supports the Darwinian idea of competitively driven divergence during speciation.