# NICHE SHIFTS AND COMPETITION IN DARWIN'S FINCHES: *GEOSPIZA CONIROSTRIS* AND CONGENERS

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The idea that interspecific competition is an important process in structuring communities stems largely from David Lack's work with Darwin's Finches (Lack, 1940, 1945, 1947, 1969). Lack made ecological inferences about feeding niches from analyses of bill sizes and shapes. He listed several instances where the niches of coexisting species were different, and where the niche of an absent species appeared to be occupied by one or more species present. These examples he interpreted as evidence of competitive displacement and exclusion.

Lack's aim was to offer a coherent theoretical framework for understanding the adaptive radiation of Darwin's Finches, not to test specific hypotheses. In contrast, our aim is to test the hypothesis of interspecific competition. This is needed because the evidence in general for interspecific competition as an important factor in determining niche relationships and community patterns has been critically debated recently (e.g., Connell, 1975, 1978, 1980; Wiens, 1977; Connor and Simberloff, 1978, 1979; Simberloff, 1978; Strong et al., 1979; Abbott, 1980; Grant and Abbott, 1980; Ricklefs and Travis, 1980; Rotenberry and Wiens, 1980; Wiens and Rotenberry, 1980). We can return to Darwin's Finches to perform such tests without circularity by obtaining and applying quan-

titative ecological data to the hypotheses, because quantitative data were not used to construct the hypotheses. In fact, Lack had almost no ecological data (see Abbott et al., 1977).

In our initial studies we analyzed ecological and morphological data from six species on eight Galápagos islands (Abbott et al., 1977; Smith et al., 1978). To follow this general approach, we selected for more detailed study three situations which have been heralded as especially clear illustrations of competitive effects (e.g., Lack, 1969; Williamson, 1972; Arms and Camp, 1979), the small size of *Geospiza fortis* on Isla Daphne Major in the absence of *G. fuliginosa* (Boag, 1981), mutually exclusive distributions of *G. fuliginosa* and *G. difficilis* (Schluter and Grant, unpubl.), and differences in bill size between populations of *G. conirostris*. Here we report the results of the third study in which we test the hypothesis of competition between *G. conirostris* and congeneric species.

## The Interspecific Competition Hypothesis Applied to *G. conirostris*

*Geospiza conirostris* occurs on Isla Española (Hood) and its satellite Gardner in the south of the archipelago, and on Isla Genovesa (Tower) in the northeast (Fig. 1). It has been recorded also on Islas Pinta
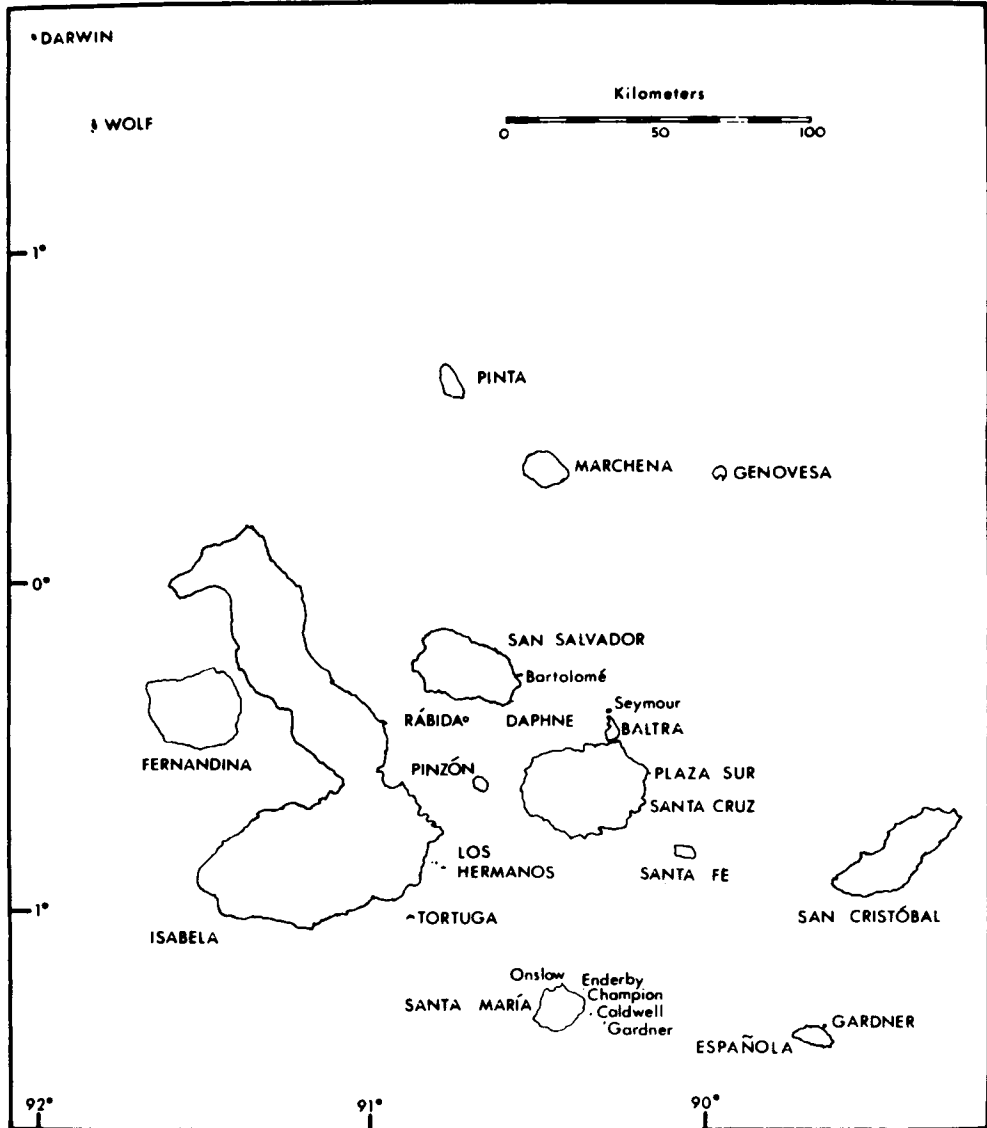
FIG. 1.   The Galápagos Islands.

(Abingdon), Wolf (Wenman) and Darwin (Culpepper), but has not been seen on these three islands recently (Harris, 1973; Bowman, 1979, and pers. comm.; D. Schluter, pers. comm.), so these latter three islands will be ignored.

Lack (1945, 1947) argued from the beak shapes of *conirostris* on Española and Genovesa that the niche on Española is a composite of the niches of absent *G. mag-* *nirostris*, *G. fortis* and *G. scandens*, and that the niche on Genovesa, in the presence of *magnirostris*, is a composite of the niches of absent *fortis* and *scandens* (Fig. 2). According to this argument, the interisland difference in the niche of *conirostris* is attributable to just one variable identified, namely the competitive influence of *magnirostris*. A competitive displacement between *conirostris* and *magnirostris* is
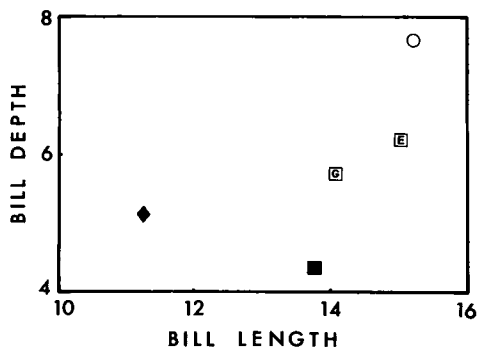
FIG. 2. Average beak size in millimeters of four finch species: *Geospiza fortis* (◆) from I. Daphne, *G. scandens* (■) from I. Daphne, *G. magnirostris* (O) from I. Genovesa and *G. conirostris* (□) from I. Genovesa (G) and I. Española (E).

also implied. Lack (1969) also proposed that *conirostris* has competitively excluded *magnirostris, fortis* and possibly *scandens* from Española, and that *fortis* and *scandens* have been competitively excluded from Genovesa by *conirostris* and/or *magnirostris*. The three species which apparently have been excluded by *conirostris* are widely distributed throughout the archipelago on almost all the major islands, including those nearest to Española and Genovesa. However *magnirostris* has become extinct on Sta. María and S. Cristóbal (see Fig. 1) since Darwin's visit to the archipelago in 1835 (Sulloway, 1982).

### Tests of the Competition Hypothesis

Testing the hypothesis is difficult for two reasons. The first is that it deals with events in the past. Historical processes cannot be tested directly in the way that contemporary processes can, except in the unlikely circumstances that the reactants are brought together under the same conditions as prevailed in the past. Instead, the hypothesis can be tested through its consequences (predictions). The assumptions upon which it rests may also be tested, and if they are shown to be wrong they must be replaced or the hypothesis must be discarded in favor of another.

The second difficulty is that Lack's argument was neither entirely explicit nor

presented in the form in which it was constructed. In his book Lack (1947) first presented his facts, then followed them with an interpretation. But Richards (1948) pointed out that there was almost as much interpretation in the presentation of facts as in the section devoted to interpretation: "It is impossible to collect or arrange scientific data without some theory which automatically introduces an element of interpretation" (Richards, 1948 p. 83). To put Lack's argument into a testable framework we must rephrase it. His observations to be explained were the distribution of species and inter-island differences in beak shape; his hypothesis was that distribution and morphology were causally influenced by interspecific competition for food; and his main assumption was that the feeding niche of a population was reflected in the average beak characteristics.

The above assumption and the corollary that diet differences parallel beak differences have been supported by the results of recent work with several species of Darwin's Finches (Abbott et al., 1977; Grant et al., 1976; Smith et al., 1978; Grant and Grant, 1979; Grant and Grant, 1980a; Grant, 1981). Therefore we might expect that *conirostris* on Española, with mean beak characteristics intermediate between those of the absent *magnirostris, fortis* and *scandens* (Fig. 2), has an intermediate feeding niche position too. However niche breadth and overlap are functions of niche size and shape as well as position (Pianka, 1969; Colwell and Futuyma, 1971; Colwell, 1979). Therefore an intermediate feeding niche position does not necessarily mean that the feeding niche of *conirostris* combines the niches of the three missing species or that the *conirostris* niche is particularly broad. For this reason we regard Lack's statements about niche similarities, differences and breadths to be testable, i.e., falsifiable predictions of the competition hypothesis. For example, if we found that *conirostris* on Española did not feed in a manner exhibited by *magnirostris, fortis* and *scandens* elsewhere, we would consider the competition hypothesis, as it is applied to the absence of these three

species, to be falsified by the failure of the prediction.

It is also predicted from the competition hypothesis that missing species would be less efficient than the species present in locating and dealing with the foods on a particular island if these missing species were to arrive. Lack (1969) used this argument when invoking the competitive exclusion hypothesis to argue for the competitive superiority of *conirostris* on Genovesa and Española, but inferiority elsewhere. We consider this to be another prediction of the hypothesis that can be tested by comparing the feeding efficiency of different species on the same species of seeds.

There are alternative explanations to the competition hypothesis for the absence of *fortis* and *scandens* from both islands and *magnirostris* from Española. One is that their food niches are not present on these islands (Bowman, 1961). We will examine this possibility when testing the niche expansion predictions. Other explanations are that they have been unable to reach the islands, and that they may have arrived in small numbers but, not finding mates of their own species, hybridized with the resident birds. We will consider these possibilities in the Discussion.

## Methods

Food supply and feeding habits of the finches vary seasonally (Smith et al., 1978; Grant and Grant, 1980a). To make meaningful inter-island comparisons we restrict our attention to data collected in the months June to August, i.e., the first half of the dry (non-breeding) season: I. Española, 8–25 August 1979, supplemented with data collected 26 May–5 June 1973 (Abbott et al., 1977); I. Genovesa, 23 June–4 August 1979; I. Daphne (no *conirostris*) 21 June–7 July 1975. We chose the early and middle dry season because beak adaptations are clearly seen then (Grant and Grant 1980a, Smith et al., 1978). Later in the dry season, i.e., from October and November onwards, *Opuntia* cactus comes into flower and all four species feed intensively on the pollen and

nectar (Grant and Grant, 1980a, 1980b; Grant and Grant, 1981). Our random sampling of seeds and fruits on the ground and on bushes, method of measuring them, and our systematic recording of feeding behavior and diets have been described in Abbott et al. (1977) and Smith et al. (1978). The only difference is that the study grid on Española was changed from the area in 1973 to one 500 m south that contained *Opuntia megasperma* trees. We did this in order to have *Opuntia* in both study areas on Española and Genovesa where feeding observations were made.

## Results

### Prediction of Niche Expansion on I. Española

To test the prediction of the competition hypothesis that the feeding niche of *conirostris* on Española combines the feeding niche of *magnirostris*, *fortis* and *scandens*, we first ask if *conirostris* feeds on the same food items taken by *magnirostris*, *fortis* and *scandens* on other islands.

Table 2 lists the plant species present on Española that are used for food by *G. conirostris* there, and by finches elsewhere in the archipelago. This table shows that many of the seeds eaten by *G. conirostris* are eaten by *magnirostris*, *fortis* and *scandens* on other islands. With the exception of *Sida spinosa* and *Alternanthera echinocephala* (Table 2), the seeds on Española which are not taken by *conirostris* but which are taken by other finch species on other islands are rare, either for natural reasons or because the plants have been largely removed by introduced goats as in the case of *Croton scouleri*. Seeds of the two exceptional species are very small and soft, they do not form an important part of the diets of *fortis* and *scandens* elsewhere, and they are not eaten by *magnirostris* elsewhere. Therefore *conirostris* on Española do feed on the same food items taken by *magnirostris*, *fortis* and *scandens* elsewhere.

A more difficult question to answer is whether a sufficient supply of seeds is available on Española for the subsistence

TABLE 1. *Ground finches present on Islas Española, Daphne and Genovesa; the mean weights in grams and bill dimensions in millimeters ( ± one standard error) of adult males, with sample sizes in parentheses. \* = measurements of live birds; all other measurements were taken from museum specimens by I. Abbott.*

| Island | Finch species | Weight | Upper mandible length | Upper mandible depth | Lower mandible width |
|---|---|---|---|---|---|
| Española | G. conirostris | 35.8 ± 0.8* (26) | 15.0 ± 0.1 (119) | 6.2 ± 0.1 (120) | 11.7 ± 0.1 (119) |
| | G. fuliginosa | 13.8 ± 0.3* (7) | 8.4 ± 0.1 (37) | 3.6 ± 0.1 (37) | 6.6 ± 0.1 (36) |
| Daphne | G. scandens | 22.0 ± 0.4* (23) | 14.9 ± 0.1* (22) | 4.7 ± 0.1* (10) | 8.9 ± 0.1* (23) |
| | G. fortis | 17.5 ± 0.4* (27) | 10.3 ± 0.1 (31) | 4.4 ± 0.1 (31) | 8.2 ± 0.1 (31) |
| Genovesa | G. magnirostris | 36.0 ± 0.8* (26) | 16.1 ± 0.2 (38) | 7.7 ± 0.2 (27) | 15.9 ± 0.1 (38) |
| | G. conirostris | 25.3 ± 0.4* (24) | 14.1 ± 0.1 (64) | 5.7 ± 0.1 (65) | 9.8 ± 0.1 (65) |
| | G. difficilis | 11.5 ± 0.1* (50) | 9.1 ± 0.1 (83) | 3.3 ± 0.0 (83) | 6.2 ± 0.0 (81) |

TABLE 2. *Plant species present on Española that have seeds eaten by finches on Española and other islands in the archipelago. Percent coverage is given on the basis of 50 random quadrats at each site. (Depth × Hardness)$^{\frac{1}{2}}$ values for seeds and percentage coverage of plants are taken from Abbott et al., 1977 and supplemented with our own data. Symbols: X = present on island; seeds eaten by M = G. magnirostris, C = G. conirostris on Española, Cg = G. conirostris on Genovesa, F = G. fortis, S = G. scandens, Ful = G. fuliginosa. Double underlining = ≥5% of feeding time spent on this food item at any one time of the year.*

| Plant species on Española | (DH)$^{1/2}$ of seeds | Percent occurrence | Seeds eaten By finches on Española | By finches on other islands |
|---|---|---|---|---|
| Cordia lutea | 13–14 | 34 | C | M |
| Opuntia megasperma | 10–11 | X | C | |
| Prosopis juliflora | 10–11 | 50 | C | M |
| Tribulus cistoides | 9–10 | X | C | M, F |
| Bursera graveolens | 4–6 | X | C | M, F, S, Cg |
| Ipomoea triloba | 3–4 | X | C | M, F, Cg |
| Neptuna plena | 3–4 | X | C | M |
| Cenchrus platyacantus | 3–4 | 2 | C | M, F, S |
| Rhynchosia minima | 3–4 | 4 | | F |
| Vallesia glabra | 2–3 | X | C | F |
| Grabowskia boerhaavifolia | 2–3 | X | | F, S |
| Lantana peduncularis | 2–3 | 14 | C, Ful | M, F, Cg |
| Desmanthus virgatus | 2–3 | 8 | C | |
| Tribulus cistoides (unripe fruit on plant) | 2–3 | X | C | F, S |
| Trianthema portulacastrum | 1–2 | 16 | C, Ful | |
| Chamaesyce recurva | 1–2 | 2 | | F, Cg |
| Croton scouleri | 1–2 | X | | M, F, Cg |
| Abutilon depauperatum | 1–2 | 4 | | M |
| Boerhaavia erecta | 0–1 | 2 | C, Ful | F |
| Cryptocarpus pyrformis | 0–1 | X | Ful | |
| Aristida subpicata | 0–1 | X | C, Ful | F, S |
| Panicum fasiculatum | 0–1 | 22 | C, Ful | F, S |
| Sida spinosa | 0–1 | 18 | | F |
| Alternanthra echinocephala | 0–1 | 20 | | F, S |

TABLE 3. *Plant species present on Genovesa that have seeds eaten by finches either on Genovesa or other islands in the archipelago. Symbols as in Table 2: D = G. difficilis.*

| Plant species on Genovesa | (DH)^{1/2} | Percent occurrence | Seeds eaten by Finches on Genovesa | Finches on other islands |
|---|---|---|---|---|
| *Cordia lutea* | 13–14 | 36 | M̲ | C̲ |
| *Tribulus cistoides* | 9–10 | X | | C̲ |
| *Opuntia helleri* | 7–8 | 8 | M̲ | |
| *Bursera graveolens* | 4–6 | 58 | M̲, Cg | F̲, S, C |
| *Ipomea linearifolia* | 3–4 | 2 | M̲, Cg | F |
| *Cenchrus platyacanthus* | 3–4 | X | M | F̲, S, C̲ |
| *Lantana peduncularis* | 2–3 | 14 | M, Cg, D | F̲, S, C̲ |
| *Heliotropium angiospermum* | 1–2 | X | D | F̲, S |
| *Chamaesyce recurva* | 1–2 | X | Cg | S |
| *Croton scouleri* | 1–2 | 44 | M̲, Cg, D | F̲, S |
| *Chamesyce amplexicaulis* | 0–1 | 4 | Cg, D | F̲, S |
| *Sida salviifolia* | 0–1 | X | D | F̲ |
| *Portulaca howelli* | 0–1 | X | | F̲, S |
| *Eragrostis cilianensis* | 0–1 | 16 | Cg, D̲ | F̲ |

of populations of *magnirostris, fortis* and *scandens*. The answer is clearest with *magnirostris*. In the dry season on I. Genovesa *magnirostris* feed almost entirely on the seeds of two species, *Cordia lutea* and *Opuntia helleri* (Smith et al., 1978; Grant and Grant, 1980*a*). *Cordia lutea* occurs about as frequently on Española as on Genovesa (Table 3). *Opuntia helleri* is more common on Genovesa than *O. megasperma* is on Española, and the seeds of *O. helleri* are smaller and softer than the seeds of *O. megasperma* (Tables 2 and 3). *Opuntia helleri* is distributed throughout Genovesa at approximately the same frequency as in the study grid (Table 3), whereas on Española *O. megasperma* is patchily distributed. However it is doubtful if the relative scarcity of *Opuntia* and hardness of the seeds are factors responsible for the absence of *magnirostris* on Espanola. First, in our five visits to Genovesa during the dry season *Cordia* seeds were more important in the diet of *magnirostris* than *Opuntia* seeds (Grant and Grant, 1980*a*). Second, the large *O. megasperma* seeds are well within the cracking range of *magnirostris* (Table 2, also see

below). Therefore the abundant supply of *Cordia lutea* seeds and the sparse supply of *O. megasperma* seeds on Española should be sufficient to sustain a population of *magnirostris* in dry seasons. In addition there are other large hard seeds such as *Prosopis juliflora* which occur abundantly throughout Española (Table 2), and although they are absent from Genovesa, they constitute a major proportion of *magnirostris* diets in the coastal areas of Isla Pinta (D. Schluter, pers. comm.).

*Geospiza fortis* subsists on a variety of small seeds in the dry season on I. Daphne prior to *Opuntia* flowering (Grant and Grant, 1980*b*). Those seeds, or close relatives, are present on Española (Table 2; see also Abbott et al., 1977). In particularly dry years on Daphne some *fortis* add the moderately hard *Tribulus cistoides* to their diet (Grant and Grant, 1980*b*). *Tribulus cistoides* is also present on Española. There is inevitable uncertainty about whether the *Tribulus* seeds are sufficiently common to sustain a population of *fortis* in the middle–late dry season in a dry year, and whether *Opuntia* flowers are sufficiently common at the end of the dry sea-

TABLE 4. *Proportion of foraging time spent on food items and feeding activities in the early dry season. Opuntia was not flowering in July and August on Española and Daphne. *Two individuals seen to crack O. helleri seeds.*

| | August 1979 Española G. conirostris | July 1975 Daphne G. fortis | July 1975 Daphne G. scandens | July 1979 Genovesa G. magnirostris | July 1979 Genovesa G. conirostris |
|---|---|---|---|---|---|
| Small seeds on ground | .291 | .464 | .490 | .087 | .197 |
| Seeds (DH)$^1$ 0–1 | | .272 | .039 | | .012 |
| 1–2 | .002 | .004 | .010 | | .029 |
| 2–3 | .064 | .034 | .191 | | |
| 4–6 | | .023 | .001 | .006 | |
| 7–14 | .295 | | | .861 | .011* |
| *Tribulus* mericarp fragments | + | .142 | .057 | | |
| *Opuntia* flower | | | | | .025 |
| *Opuntia* aril | .040 | .034 | .191 | .045 | .495 |
| *Opuntia* pad ripping and probing for arthropods | .280 | .020 | .005 | | .036 |
| *Opuntia* spine base | .001 | .001 | .009 | | |
| Bark ripping | .027 | | | | .157 |
| Gleaning | | | .005 | | .039 |
| Sulidae egg | | .006 | .004 | .001 | |
| Total seconds | 26,135 | 20,266 | 5,285 | 12,255 | 19,416 |

son. But given the large range of alternative foods for *fortis* on Española, we conclude that a population of *fortis* could be sustained there.

*Geospiza scandens* feeds on small seeds and cactus products. In years such as 1975, when there is abundant rainfall during the wet season, small seeds are plentiful in the dry season and these are taken from plants and from the ground (Table 4). *Geospiza scandens* then turns to *Opuntia* pollen and nectar when flowers start blooming in October (Smith et al., 1978; Grant and Grant, 1980b). In the dry season in dry years on Daphne it feeds largely on *Opuntia echios* seeds and arils; for example, the proportion of time spent foraging on these items was .900 in August of 1980, a relatively dry year. On Española the large and hard seeds of *Opuntia megasperma* are certainly beyond the cracking power of *scandens*, and the aril is fibrous and less rewarding than the succulent arils of *Opuntia* seeds elsewhere. Despite these observations, a *scandens* population could be self-sustaining on Española through a diet of small seeds and insect larvae taken from *Opuntia* pads, because on Isla Marchena, where *Opuntia helleri* reproduces mainly vege-

tatively and flower production and seed set are low, *G. scandens* feeds mainly on diptera larvae extracted from rotting *Opuntia* pads in the dry season (D. Schluter, pers. comm.). On Isla Champion off Floreana, *Opuntia megasperma* var. *megasperma* is abundant, and like *O. megasperma* var. *orientalis* on Española, the aril is fibrous, but the seeds are even harder. In August 1980 we recorded *G. scandens* feeding for proportionately 56.8% of its foraging time on beetle larvae and pupae from rotting *Opuntia* pads (see also Table 4 for data from Daphne). We found many beetle larvae and pupae in *Opuntia* pads on Española.

Not one of the three species, *magnirostris, fortis* or *scandens,* is dependent upon one or more food types that are lacking on Española, and several of their diet items are present. The evidence contradicts the hypothesis that the three species are absent because suitable foods are lacking.

### The Prediction of Niche Expansion on I. Genovesa

To test the prediction that the feeding niche of *conirostris* on Genovesa combines the feeding niche of *fortis* and *scan-*

*dens* we follow the same argument concerning missing species on Española. That is, we first ask if Genovesa *conirostris* feed on the same food items as missing *fortis* and *scandens* do on other islands. Table 3 lists the plant species on Genovesa and the diets of present and absent finch species. It shows that many food items or else close relatives present on Genovesa which are consumed by *conirostris* are eaten by *fortis* and *scandens* on other islands.

The question of whether there is sufficient food on Genovesa to support a population of *fortis* and *scandens* can be answered with a similar argument to the one presented above concerning the absence of *fortis* and *scandens* on Española. Plants are widely distributed throughout Genovesa (Grant and Grant, 1980a) at approximately the same frequency as in the study grid (Table 3). Many small seeds present and common on Genovesa are consumed by *fortis* and *scandens* elsewhere (Table 3). Although *O. helleri* seeds are hard and beyond the cracking powers of *fortis* and *scandens,* the aril is fleshy and succulent and similar to the aril of *O. echios* which is eaten by *fortis* and *scandens* on Daphne (Table 4). *Opuntia helleri* is abundant and flowers bloom profusely from November to May (Grant and Grant, 1980a) and would provide pollen and nectar for both species. Rotting *Opuntia* pads contain diptera larvae. Thus a diet of small seeds, *Opuntia* arils and pollen would be available for *fortis* on Genovesa. This is similar to the diet of *fortis* on Daphne. If *scandens* can subsist on Marchena and Champion on dry season diets of small seeds and arthropod larvae taken from *Opuntia* pads, they could surely survive on Genovesa where in addition to a supply of small seeds *Opuntia* is common and would provide arils, diptera larvae, pollen and nectar. Therefore many food items present on Genovesa are consumed by *fortis* and *scandens* elsewhere, and there are no known essential constituents missing. So there is no reason to suppose *fortis* and *scandens* are absent from Genovesa because their foods are not present.

We have found that the range and abundance of food plants present on Española and Genovesa should be sufficient to support populations of *fortis* and *scandens* on both islands and *magnirostris* on Española. We now ask if *conirostris* feeding niches combine the feeding niches of the missing species and answer this by comparing the feeding niches of *conirostris* with the feeding niches of the missing species on other islands in a similarity analysis.

### Comparison of Allopatric Feeding Niches

Table 4 shows the proportion of feeding time spent on various food items in July and August. Several parts of *Opuntia* as well as seeds are a source of food for the finches, particularly *scandens* and *conirostris.* Therefore *Opuntia* feeding must be considered, together with seed consumption, in a comparison of feeding niches. Seeds have been grouped into depth-hardness classes for comparative purposes, except that the mericarps (fruit parts) of *Tribulus cistoides* have been considered separately because of the unique problems they pose to birds (Grant, 1981a). The result is a classification of proportional feeding in 14 categories. Grouping seeds into a few size categories could bias the results in favor of greater similarity. We believe that bias is minimal because many of the seeds within one category are from the same plant species on different islands. Where they are not, all the seed species within the category are eaten by both species being compared on at least one island in the archipelago. For example, seed size-hardness category 7–14 includes *Opuntia helleri* and *Cordia lutea* on Genovesa, and *Opuntia megasperma, Prosopis juliflora* and *Cordia lutea* on Española. *Geospiza magnirostris* eats *O. helleri* and *C. lutea* seeds on Genovesa and *Prosopis juliflora* on Pinta. *Geospiza conirostris* takes all three species on Española.

To compare feeding niches we use the index of similarity $1-0.5 \ (\Sigma |p_{1i} - p_{2i}|)$ where $p_{1i}$ and $p_{2i}$ are the proportions of foraging time spent by the two species on

TABLE 5. *Similarities in the foraging of pairs of* Geospiza *species observed over 8-day periods.*

| | | | |
|---|---|---|---|
| Española *G. conirostris* | v | Genovesa *G. conirostris* | SIM = .31 |
| | v | Daphne *G. fortis* | SIM = .38 |
| | v | Daphne *G. scandens* | SIM = .40 |
| | v | Genovesa *G. magnirostris* | SIM = .42 |
| | v | Española *G. fuliginosa* | SIM = .37 |
| | v | *G. magnirostris* and *conirostris* | SIM = .53 |
| | v | *G. scandens* and *fortis* | SIM = .41 |
| | v | *G. magnirostris, fortis* and *scandens* | SIM = .65 |
| Genovesa *G. conirostris* | v | Genovesa *G. magnirostris* | SIM = .14 |
| | v | Daphne *G. fortis* | SIM = .27 |
| | v | Daphne *G. scandens* | SIM = .42 |
| | v | *G. fortis* + *scandens* | SIM = .30 |

food items classified in Table 4. This is appropriate for discrete classes of food items not measured along a common scale (Whittaker, 1960). We do not have comparable estimates of nectar, pollen, aril, arthropod and seed density; therefore we are unable to use Hurlbert's (1978) method of comparing diet similarity in relation to food availability. Table 5 gives the similarities based on the combined observations of eight successive days. There are no confidence limit estimates on the similarity values, but the values are not close to 0 and 1 where sampling distortions are likely to be greatest (Ricklefs and Lau, 1980). Figure 3 shows cumulative similarities over a period of eight successive days. The stability of the similarities after about five days suggests that our results would not have been very different if we had extended the period of observation.

Española *conirostris* is closest in feeding habits to *magnirostris* (similarity = .42). This results from both species taking large and hard seeds. The difference is due to Espanola *conirostris* also taking small seeds and ripping open *Opuntia* pads to feed on dipteran larvae and pupae. In this respect Española *conirostris* resemble *fortis* and *scandens*. And in fact, in agreement with the prediction of the competition hypothesis, the feeding niche of Española *conirostris* is more similar to an unweighted composite of *magnirostris, fortis* and *scandens* niches on other islands than it is to the niches of these three species treated separately, to

the niche of conspecific *conirostris* population on Genovesa, or to any pairwise combinations of niches of these species (Table 5). Furthermore Española *conirostris* has the greatest niche breadth (Table 6).

The competition hypothesis also predicts that the feeding niche of Genovesa *conirostris* is more similar to the composite niche of *fortis* and *scandens* than to the niches of these two considered separately or to the niche of the *conirostris* population on Española. This prediction is not fully realized (Table 5). The niche of Genovesa *conirostris* is most similar to the niche of *scandens* considered alone. The composite niche of *scandens* and *fortis,* the niche of *fortis* alone and the niche of Española *conirostris* are all about equally similar to the niche of Genovesa *conirostris*. Reference to Table 4 will show the reasons for these results. Genovesa *conirostris* is similar to *scandens* because both exploit *Opuntia,* but *conirostris* spends more time ripping the bark off *Bursera* and *Croton* branches to get at arthropods, mainly termites, and less time feeding on small seeds on the ground than *scandens* does. The similarity between *conirostris* and *fortis* is lower because *fortis* exploits *Opuntia* parts less and small seeds on the ground more than both *scandens* and *conirostris.*

Thus the evidence shows that the *conirostris* niche on Genovesa is similar to the *scandens* niche but does not support the prediction that it is similar to a composite
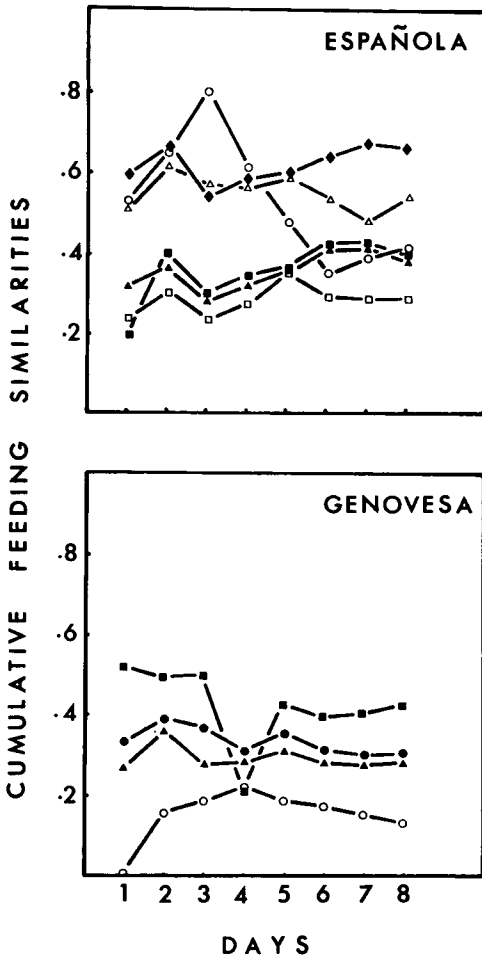
**FIG. 3.** Similarities in feeding niches between species, calculated from observations made on day 1, day 1 + 2, day 1 + 2 + — + $n$ over 8-day periods. Similarities are between *G. conirostris* on I. Española (above) or I. Genovesa (below) and the following: *G. magnirostris* (O), *G. fortis* (▲), *G. scandens* (■), *G. conirostris* on I. Genovesa (□), *G. fortis* and *G. scandens* combined (●), *G. magnirostris* and *G. conirostris* combined (△) and *G. magnirostris*, *G. fortis* and *G. scandens* combined (◆). *G. conirostris* on I. Española is most similar to *G. magnirostris*, *G. fortis* and *G. scandens* combined, but *G. conirostris* on I. Genovesa is most similar to *G. scandens* alone.

*fortis* and *scandens* niche. Note too in Table 6 that the niche of Genovesa *conirostris* is not particularly broad or diverse.

### Comparison of Sympatric Feeding Niches

The hypothesis of a competitive displacement of *magnirostris* and *conirostris*

**TABLE 6.** *Measurements of feeding diversity* $1/\Sigma\ p_i^2$ *and niche breadth* $\bar{H}/H_{max}$ *of Geospiza species. These are alternative measures of the variation in feeding characteristics of each species.* $p_i$ *is the proportion of feeding time spent on the ith food item.* $\bar{H} = -\Sigma p_i\ log_{10}p_i$ *and* $H_{max} = log_{10}S$ *where* $S =$ *the number of food items taken. Data are from Table 4.*

|  | Feeding diversity | Niche breadth |
|---|---|---|
| Española *conirostris* | 3.96 | 0.90 |
| Daphne *fortis* | 3.20 | 0.63 |
| Genovesa *conirostris* | 3.19 | 0.68 |
| Daphne *scandens* | 3.14 | 0.61 |
| Genovesa *magnirostris* | 1.33 | 0.32 |

on I. Genovesa predicts a low similarity in feeding niches between these two species. It also predicts that the two *conirostris* populations differ in their feeding niches in such a way that *magnirostris* feeds on items taken by *conirostris* on Española but not by *conirostris* on Genovesa.

Our results (Table 5) support these predictions. There is a particularly low similarity between *magnirostris* and *conirostris* on Genovesa, lower than any other pair of species compared. The similarity between the two *conirostris* populations is also low, but when Española *conirostris* is compared to a composite of Genovesa *conirostris* and *magnirostris* the similarity rises to .53. Reference to Table 4 shows the reason for these results. The low similarity between *magnirostris* and Genovesa *conirostris* is due to *magnirostris* feeding almost entirely on large-hard seeds, whereas *conirostris* exploits *Opuntia* parts and arthropods. The two populations of *conirostris* differ in four ways. The first is a discrete difference. Española *conirostris* feeds on large hard seeds, Genovesa *conirostris* does not. The three other differences are ones of degree. *Opuntia helleri* arils on Genovesa are succulent and abundant, and are taken more frequently than are the comparatively dry and fibrous arils of *O. megasperma* on Española. Also on Genovesa the tip-biting, twisting, tearing motion employed to strip bark off trees to reach arthropods is more highly developed, and occurs more frequently, than on Española. This is a habit employed fre-

TABLE 7. *Measurements in millimeters of random, cracked and rejected* Cordia lutea *seeds on I. Española and I. Genovesa.*

| Island | Sample | Length | | Depth | | Length × depth | |
|--------|--------|--------|--------|--------|--------|--------|--------|
| | | $N$ | $\bar{x} \pm SE$ | $N$ | $\bar{x} \pm SE$ | $N$ | $\bar{x} \pm SE$ |
| Española | Random | 106 | 10.3 ± 0.1 | 106 | 6.1 ± 0.1 | 106 | 63.2 ± 1.4 |
| | Cracked by | | | | | | |
| | G. conirostris | 108 | 8.8 ± 0.1 | 108 | 5.3 ± 0.1 | 108 | 46.5 ± 1.0 |
| Genovesa | Random | 59 | 10.4 ± 0.2 | 59 | 6.8 ± 0.1 | 59 | 71.5 ± 1.9 |
| | Cracked by | | | | | | |
| | G. magnirostris | 54 | 9.6 ± 0.2 | 54 | 6.3 ± 0.1 | 54 | 59.9 ± 1.9 |
| | Rejected by | | | | | | |
| | G. magnirostris | 22 | 9.7 ± 0.3 | 22 | 6.3 ± 0.2 | 22 | 61.6 ± 2.8 |

quently by a tree finch with a similar beak size and shape, *Camarhynchus psittacula,* on other islands such as Pinta, Marchena and Santa Cruz (unpubl. observ.). Finally *Opuntia* pad ripping was rare on Genovesa in July yet quite common on Española in August. However it was common on Genovesa in November, (Grant and Grant, 1979; Grant and Grant, 1980a). In this instance, the difference between the niches of the two populations may be a little exaggerated because niches change seasonally and our observations on the two islands were not made at exactly the same time of the year.

*Food Selection and Feeding Efficiency*

To test the prediction that missing species would be less efficient than species present in dealing with foods, we concentrated on the feeding of adults of Española *conirostris* and Genovesa *magnirostris* upon a common food type, the seeds of *Cordia lutea. Cordia lutea* seeds were chosen because the stones or pits that contain them (Wiggins and Porter, 1971) are the largest and hardest of the fruits and seeds taken both by *conirostris* on Española and *magnirostris* on Genovesa. They are a major dry season food item in the diets of both species and for this reason, and because they are large and hard, they are most likely to reveal any difference in feeding efficiency between the two species (Grant et al., 1976). We collected and measured random samples of stones from the ground, the remains of all cracked stones found which were intact enough to permit measurement and, on Genovesa,

all stones seen to be picked up and rejected without cracking by *magnirostris.* Table 7 gives the measurements, and Table 8 gives the results of statistical comparisons.

*Cordia* stones are larger on Genovesa than on Española, but on both islands birds tend to select the small stones. *Geospiza magnirostris* rejected stones of the same size as the ones they cracked, therefore the basis of rejection in this small sample must have been something other than size. Many of the stones seen to be rejected had emergence holes of a bruchid beetle, *Amblycerus galapagoensis* so this was possibly the reason for rejection. Eighty-five percent of the random sample of *Cordia* stones on Genovesa had larvae of this beetle; the larvae are eaten by *magnirostris* (and also by *conirostris* on Española). The rejected stones without emergence holes were not particularly large. Therefore the difference in size between stones cracked and stones at large reflects a selection by the finches that does not involve handling. In this case size is probably the cue used.

How would *magnirostris* perform on Española? The average size (length × depth) of *Cordia* stones cracked by *magnirostris* on Genovesa is not significantly different from the average size of stones on Española ($t_{158} = 1.10, P > .1$). Therefore *magnirostris* would probably not be size-selective on Española. In contrast to this result, if Española *conirostris* were present on Genovesa it would be able to crack only the smallest *Cordia* stones, as indicated by a comparison of a random

TABLE 8. *Differences between samples of* Cordia lutea *tested by* t *tests. One to three asterisks indicate statistical significance (<.05, <.01 and <.001, respectively). Log-transformed data were used to test for a difference between random and cracked seeds on Española (length × depth) because variances were unequal.*

| Island | Sample | Length | | Depth | | Length × depth | |
|---|---|---|---|---|---|---|---|
| | | d.f. | t | d.f. | t | d.f. | d.f. |
| Española | Random vs. cracked by G. conirostris | 188 | 7.00*** | 141 | 3.21** | 21.2 | 9.99*** |
| Genovesa | Random vs. cracked by G. magnirostris | 111 | 3.81*** | 111 | 3.43*** | 81 | 5.79*** |
| Genovesa | Random vs. rejected by G. magnirostris | 79 | 2.41* | 79 | 2.51* | 79 | 2.84** |
| Genovesa | Cracked by G. magnirostris vs. rejected by G. magnirostris | 74 | 0.35 | 74 | 0.08 | 74 | 0.30 |
| Española vs. Genovesa | Random | 163 | 0.48 | 163 | 5.67*** | 163 | 3.44*** |
| Española vs. Genovesa | Cracked | 160 | 4.31*** | 89 | 4.57*** | 160 | 7.97*** |

sample of stones from Genovesa and the sample cracked by *conirostris* on Española ($t_{160}$ = 7.97, $P$ < .001). This is further illustrated in Figure 4. It is not surprising, in view of this result, that the small-billed form of *conirostris* which does occur on Genovesa (Fig. 2) does not crack stones of *Cordia lutea*.

Not only do *magnirostris* on Genovesa take larger *Cordia* stones than *conirostris* on Española, they take much less time on average to crack them (13.6 ± 2.6 s, $N$ = 36) than *conirostris* on Española (24.2 ± 3.3 s, $N$ = 45; $t_{79}$ = 3.25, $P$ < .001). However the total handling time on *Cordia* stones is not significantly different ($P$ > .1) between *conirostris* (89.7 ± 10.3 s, $N$ = 45) and *magnirostris* (71.6 ± 6.5 s, $N$ = 44). Total handling time refers to the period of time between picking up a stone and finishing feeding on the seed or beetle larva. We did not include searching time and we did not detect any difference in the time taken to extract seeds and larvae. Overall the total efficiency of *Cordia* seed exploitation is approximately the same in the two species, in terms of energy intake per unit of energy expended.

A very small difference in metabolism between the species is suggested by the small difference in body weights in Table 1. Thus if *magnirostris* was on Española

it would have slightly higher energetic costs through being slightly larger. But this disadvantage would probably be more than offset by two feeding advantages; it would presumably handle the small *Cordia* stones slightly faster than *conirostris,* and it would be able to deal quickly with the large *Cordia* stones which *conirostris* has difficulty in cracking or else avoids. Small differences in metabolism would only be important if, in addition, *magnirostris* were much poorer at finding *Cordia* stones than *conirostris,* in which case energetic costs of searching would be much higher in *magnirostris* than *conirostris.*

Figure 5 shows that the advantage possessed by *magnirostris* over *conirostris* in cracking *Cordia* stones is held, although to a lesser extent, with smaller and softer seeds. In this figure, the average time each species takes to crack a seed is seen to rise with an increase in seed size and hardness. Unfortunately the number of points for each finch species is too small for analysis by regression, and pairwise comparisons of finch species are limited by the small number of seeds of a given type eaten by two species. The main point we wish to make is that there is no detectable reversal of the relative efficiencies of *magnirostris* and *conirostris* towards the lower end of the seed size-hardness scale. A graph of
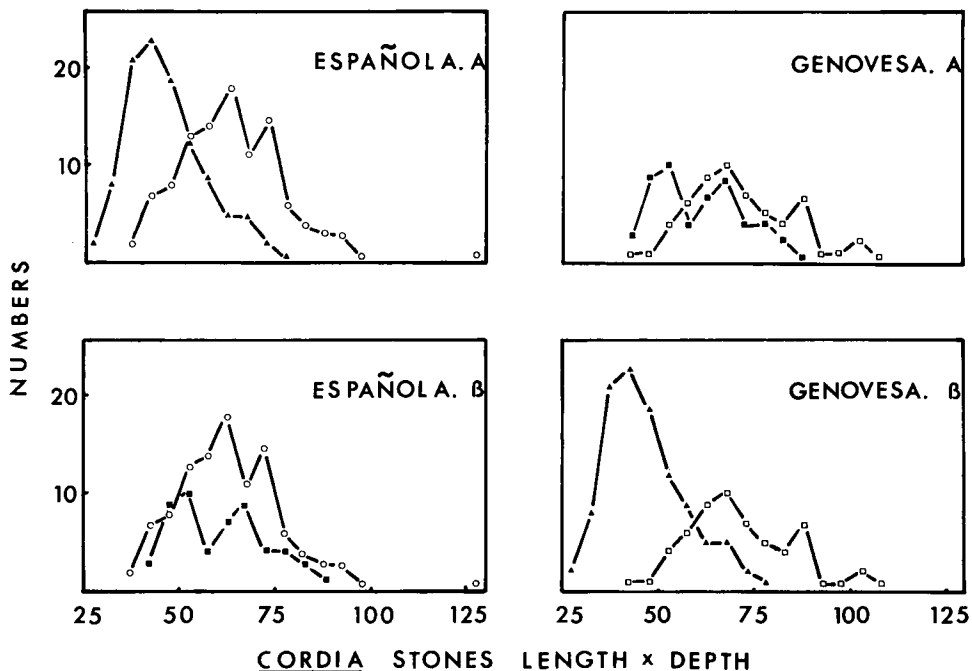
FIG. 4. Frequency distributions of the sizes of *Cordia lutea* stones measured in two dimensions in millimeters. On I. Española the stones sampled at random (O) are compared with those cracked by *G. conirostris* (▲) in A, and with the superimposed distribution of seeds cracked by *G. magnirostris* (■) on I. Genovesa in B. On I. Genovesa the stones sampled at random (□) are compared with those cracked by *G. magnirostris* (■) in A and with those cracked by *G. conirostris* (▲) on I. Española in B.

seed handling times plotted against seed size-hardness gives the same results.

Figure 5 also shows that *conirostris* has a feeding efficiency advantage over *fortis* (without taking metabolic requirements into account). Thus the prediction of the competition hypothesis that *conirostris* has a feeding efficiency advantage over *fortis* is found to be correct, but the prediction that *conirostris* has a feeding efficiency advantage over *magnirostris* was not supported by our results; rather *magnirostris* appears to have an advantage over Española *conirostris*. A necessary qualification is that if immigrant *magnirostris* were immatures, they might be at a feeding efficiency disadvantage in relation to adult *conirostris*, because on Genovesa immature *magnirostris* take significantly longer to crack *Cordia* stones ($36.9 \pm 8.15$, $N = 4$) than do adult *magnirostris* ($t_{38} = 3.83$, $P < .001$).
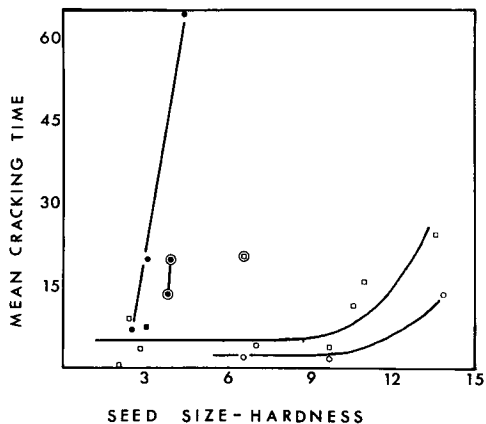


FIG. 5. The average time in seconds to crack seeds and fruits of several plant species as a function of the size and hardness of those seeds as indexed by the square root of the depth in millimeters × the hardness in kgf. The finch species are *G. magnirostris* from I. Genovesa (O), *G. scandens* from I. Daphne (■), G. fortis from I. Daphne (●) and from I. Santa Cruz (◉) where it is larger (Grant et al., 1975), and *G. conirostris* from I. Española (□) and from I. Genovesa (◎). Curves have been fitted by eye.

## DISCUSSION

The interspecific competition hypothesis has been supported by several but not all of our observations. Our ecological data support Lack's hypotheses that *fortis* and *scandens* have been competitively excluded from Española by *conirostris*; that *scandens* has been competitively excluded from Genovesa by *conirostris*; and that competitive character displacement between *conirostris* and *magnirostris* could have occurred on Genovesa. The evidence does not support the view that *fortis* has been excluded by *conirostris* from Genovesa, or that *magnirostris* has been excluded by *conirostris* from Española. We will first discuss the main assumptions upon which these conclusions rest, then consider alternative explanations for our results and finish by pointing out two implications of our study.

We have assumed that an equal weighting of niches is appropriate for the comparison of *conirostris* niches with the combined niches of missing species. An unequal weighting may be more realistic, perhaps based upon degree of bill size and shape similarities, but this would not alter the results strongly. Second, we have assumed that the results are not substantially affected by the particular allopatric populations used in comparisons with *conirostris*. This assumption is especially important in our use of *magnirostris* data, since those data come from an island where one population of *conirostris* is present. Our *magnirostris* data from Genovesa in July (this study) and November (Grant and Grant, 1980*a*) are similar to *magnirostris* data from I. Pinta and I. Marchena (D. Schluter, pers. comm.) and I. Santa Cruz (Smith et al., 1978) in showing that large and hard seeds predominate in dry season diets. Beak sizes of *magnirostris* on these islands are similar (see Lack, 1947). Therefore we believe this assumption is approximately correct.

Third, we have assumed that the results are not dependent upon which year we studied the finches. Since year-to-year variation in rainfall, plant production and seed availability can produce annual shifts in feeding niches (Grant and Grant, 1980*b*), our results may be partly dependent on the relatively plentiful food supply in the years of our study. We have tried to eliminate this bias as much as possible by restricting our comparisons to years when there was comparable rainfall in the preceding wet season on all study islands. Rainfall in 1975 was above average on Daphne (Grant and Boag, 1980), and in 1979 about average on Genovesa and Española. But even in years of substantial rainfall, food supply limits population sizes during the dry season (Smith et al., 1978). In dry years this limiting influence is especially strong (Boag and Grant, 1981). It would be preferable to make inter-island comparisons in a dry year, but the only data we have from a dry year comes from Daphne (Grant and Grant, 1980*b*; Boag, 1981; Boag and Grant, 1981).

A fourth assumption is that other potential biotic factors not considered, such as disease and predation, can be ignored. Very little is known about disease, and nothing is known to suggest that it would be an important factor on one island and not on another. The three main predators are the Galápagos hawk *Buteo galapagoensis* (deVries, 1976), and the short-eared owl *Asio flammeus* (Grant et al., 1975; Grant and Grant, 1980*a*) and mockingbirds *Nesomimus* spp. (Downhower, 1978; Grant and Grant, 1980*a*). The owl is present on all our study islands, mockingbirds are present on both Española and Genovesa, but the hawk is present on only Española. From this it could be argued that *magnirostris* is predator-excluded from Española, but this would be inconsistent with the coexistence of *magnirostris* and hawks on other islands (Lack, 1947; Harris, 1973), and would presumably require a preferential predation upon *magnirostris* for reasons of its slightly larger size or its rarity.

A fifth assumption is that the inferred competition is with the specified species and not with others. This may be incorrect. Since Lack's (1969) last treatment of the subject, MacArthur (1972) and

MacArthur et al. (1972) have drawn attention to the competitive influence of many species upon one, and introduced the term diffuse competition to describe it. In the present context *magnirostris*, *fortis* and *scandens* may be absent from Española for reasons of competition with *conirostris*, *fuliginosa*, *Nesomimus macdonaldi* (mockingbird) and *Zenaida galapagoensis* (dove). Likewise the absence of *scandens* and *fortis* from Genovesa may be due to the combined influence of *magnirostris*, *conirostris*, *difficilis*, *Nesomimus parvulus* and *Zenaida galapagoensis* or some combination of these species (e.g., *conirostris* and *magnirostris*: Lack, 1969). All eat seeds and *Opuntia* parts, and all show a divergence in diets from wet season to dry season which suggests an avoidance of competition (Grant and Grant, 1980*a*). The remaining land bird species on these islands, *Certhidea olivacea*, *Dendroica petechia* and *Myiarchus magnirostris* (Española only), can be ignored because they have diets of arthropods and are therefore not likely to compete with the others.

The data in Tables 2 and 3, combined with data in Abbott et al. (1977), Smith et al. (1978) and Grant and Grant (1980*a*), make the possibility of diffuse competition plausible, because they show that some foods taken frequently by *fortis* elsewhere are taken frequently by *fuliginosa* on Española and by *difficilis* on Genovesa; Lack (1969) ignored these two species in his analyses. The hypothesis of diffuse competition is extremely difficult to test (Abbott and Grant, 1976), nevertheless we must acknowledge that it could succeed in explaining the absence of *fortis* from Genovesa where the hypothesis of competition with *conirostris* fails.

Finally we have assumed that changes in the vegetation of Española caused by goats introduced in the last century have not created a bias in our comparisons with the undisturbed islands of Daphne and Genovesa. Such a bias could arise if current *conirostris* morphology and feeding were adapted more to past pre-disturbance conditions on Española than to modern post-disturbance conditions. However, the argument that bills of contemporary *conirostris* are adapted to past conditions is difficult to sustain in the face of evidence of rapid morphological change in a population of *fortis* under selection for large bill size (Boag and Grant, 1981). If the altered vegetation resulted in a change in *conirostris* phenotype it probably occurred in the last century: we have been unable to detect a change this century in comparisons between specimens collected in 1905–06 and modern ones.

Even though the competition hypothesis has been largely supported by the results of the tests and its assumptions are reasonable, other hypotheses may be just as good or better. We now consider three other hypotheses.

The first alternative is that species are absent from an island because their food niches are absent. For example, Bowman (1961 p. 286) wrote "the nature of the vegetation on Hood Island [Española] is such that possibly there are too few hard-coated seeds to support a population of *G. magnirostris*, and too few *Opuntia* cactus plants to support *G. scandens.*" Presumably this explanation can be extended to account for the absence of *fortis* as well. The hypothesis was tested in our study and found to be incorrect. These species are not absent from Española because of the absence of an appropriate food supply, nor are *fortis* and *scandens* absent from Genovesa for that reason.

The food supply hypothesis has been invoked by Bowman (1961) to explain differences in feeding niches a) between coexisting species, such as *conirostris* and *magnirostris* on Genovesa, and b) between populations of the same species on different islands, such as *conirostris* on Genovesa and Española. It is succinctly stated as follows: "Anatomical differences between closely related species on any one island are best thought of as biological adjustments which have been evolved when the forms were in isolation. These adjustments could have prevented 'competition' from occurring between the forms when subsequently they came together on the

same island" (Bowman, 1961 p. 296). Therefore, *conirostris* populations differ in beak morphology and diets because they have become adapted to the different food supplies the islands possess, and coexisting *conirostris* and *magnirostris* populations on Genovesa differ because their adaptations occurred originally on different islands.

This hypothesis, like the competition hypothesis, rests on the assumption that diet and beak shape are correlated, hence feeding niches are correctly inferred from beak morphology. Bowman (1961) presented empirical evidence to support this assumption as it applies to differences between coexisting species, but not as it applies to inter-island differences within species. The food supply hypothesis has the additional merit of constituting a null alternative (no interaction) to the competition hypothesis (Abbott et al., 1977; Strong et al., 1979; Grant and Abbott, 1980). It has two serious problems, however, that make it useful only to the extent that other hypotheses fail.

The first problem is that it is doubtful if there are enough islands in the archipelago for all sympatric populations to have evolved their adaptations for food gathering in isolation from each other, i.e., allopatrically. This makes the hypothesis unreasonable in its more general, all-embracing form, but it could still be correct in specific instances. The second problem is that it explains the absence of a species from an island by the absence of the appropriate food supply, yet it allows for adaptation of new colonists to a local food supply which differs from the supply on the island of origin. With such comprehensiveness it is close to being unfalsifiable. The dividing line between conditions that preclude establishment of colonists and conditions that allow establishment and persistence long enough for adaptation to take place needs to be specified, but it would be extremely difficult to do so operationally (see also Grant, 1975). Because of these difficulties we placed greater emphasis in this paper on testing the competition hypothesis. Results of the test generally supported the competition hypothesis, and we have no reason to turn to the operationally more complex food hypothesis to explain morphology and distribution of the finches.

A second explanation for the absence of *fortis* and *scandens* from both islands and *magnirostris* from Española is that they have not been able to reach these islands. These two islands may be relatively inaccessible to birds by virtue of their positions in relation to neighboring islands (see Fig. 1) and prevailing winds (Power, 1975). This explanation for species absences has been repeatedly rejected on the grounds that inter-island wanderings are quite frequent (Lack, 1947, 1969; Bowman, 1961; Harris, 1973). For example, 15 *fortis* individuals were collected on Española in 1906, and I. Abbott (pers. comm.) observed one in June 1973. One individual has been collected on Genovesa, and we observed two there in July 1979 (see also Yang and Patton, 1981). We also netted an adult male *scandens* on Genovesa at the same time and one individual has been collected 20 miles from the nearest island (Gifford, 1919). *Geospiza magnirostris* also make inter-island movements (Grant et al., 1975).

A third hypothesis for the absence of breeding populations of species on Española and Genovesa is that the few individuals who reach the islands and survive to the breeding season fail to find conspecific mates and hybridize with members of one of the resident species. We refer to this as the immigrant-hybridization hypothesis. For example, it is plausible that small numbers of *magnirostris* hybridizing with *conirostris* have been partially responsible for the more *magnirostris*-like features in the Española *conirostris* bill. We do not know if hybrid offspring would be viable, but viability is likely because two *magnirostris* × *conirostris* pairs produced viable offspring on Genovesa in 1980 and 1981 (unpubl. observ.). A parallel situation occurs on Daphne. *Geospiza fuliginosa* has repeatedly immigrated since our study began there in 1973. It has not established a breeding population but a few individuals

have hybridized with the resident larger species *G. fortis* (Boag, 1981; Grant and Price, 1981). *Geospiza fortis* are unusually small on this island.

Hybridization might also occur between two species if one becomes rare: the few individuals of the rare species then court heterospecifics in the virtual absence of conspecifics. An unbalanced sex ratio in the common species (cf. Boag and Grant, 1981) could facilitate the acceptance of heterospecific mates. We refer to this alternative as the resident-hybridization hypothesis. It may be invoked to explain the absence of *magnirostris* from Española by supposing that *magnirostris* was once present and common, became rare, hybridized with *conirostris* and disappeared as a species.

Some support for the hypothesis is provided by the particularly large form of *magnirostris* on the neighboring islands of Santa María and S. Cristóbal. It was once common but became extinct on both islands sometime after Darwin's visit in 1835 (Steadman, 1981; Sulloway, 1982). A few museum specimens of intermediate size from these two islands (e.g., see Sulloway, 1982) suggest that *magnirostris* and *fortis* hybridized during the period of decline of the *magnirostris* populations. By the time Española was first visited by collectors at the end of the nineteenth century, *magnirostris* was already extinct (or exceedingly rare) on the other two islands. If it had been present earlier on Española as well, it would have been larger than *conirostris* in bill dimensions by much more than 15%, which is the minimum difference between currently coexisting species in the archipelago (Grant, 1981*b*). Even the smaller form of *magnirostris* on Santa Cruz is larger than *conirostris* in bill depth by more than 15%.

Why did the two, possible three, populations of *magnirostris* go extinct? The large bill may have been adapted to cracking the particularly large and hard seeds of *Opuntia megasperma*. This species of *Opuntia* has the largest and hardest seeds of any *Opuntia* species in the archipelago; the size-hardness index is 10.9 on Espa-

ñola and more than 20 on Champion (unpubl. data) in contrast to a range of 2 to 7 for the other species (Grant and Grant, 1981). The species is present on only the three southern islands and their satellites. Populations of *Opuntia* were decimated in this century and the last one by human destruction of natural habitat on Santa María and S. Cristóbal, and by introduced goats on all three islands. Nowadays, *O. megasperma* only grows in large stands on the goat-free islets of Champion and Gardner off Santa María. Thus direct and indirect effects of human activity probably caused the demise of the *magnirostris* populations, although we have no detailed knowledge of why they were not sustained by alternative foods such as the seeds of *Cordia lutea* and *Prosopis juliflora*.

The changes occurring on the southern islands in both habitat and finch populations in the last 150 years have been so poorly documented that most of these ideas about past hybridization will remain as speculation. The hypothesis will be supported, however, if fossils of *magnirostris* and of intermediates with *conirostris* are found on Española; fossils of *magnirostris* have recently been found on Santa María (Steadman, 1981). The immigrant-hybridization hypothesis can be investigated directly, at least in principle. However, *magnirostris* was not recorded on Española by collectors at the turn of the century (e.g., Gifford, 1919), or in recent field studies (Abbott et al., 1977; Downhower, 1978; this study). The role of hybridization in the evolution and distribution of the finches remains an open question.

We conclude by making a general point that emerges from this discussion. Biogeographic analyses have made an important contribution already by showing how widespread competitive effects might be (Lack, 1947, 1976; Diamond, 1972, 1975; MacArthur, 1972; Brown, 1975; for criticism see Connor and Simberloff, 1978, 1979; Simberloff, 1978; Strong et al., 1979), but we believe that because interspecific competition is an ecological process, ecological studies are required to test the hypothesis. The present study has provided

some ecological tests but it has also identified areas of ignorance that deserve attention not only among Darwin's Finches but in all similar studies of island communities.

The first is the colonization of islands or, to be more general, the entry of new species into a community. In the case of Darwin's Finches, most inter-island wanderers are first-year birds. As many as 100 or more may arrive on an island following one breeding season, and invariably all leave (or die) before or during the next breeding season (Grant et al., 1975; unpubl. observ. on I. Daphne). They do not have sub-normal weights, and with few exceptions they do not exhibit reproductive behavior if they stay up to the beginning of the breeding season. Factors other than interspecific competition for food are likely to influence the decisions of individuals to stay or to leave. These factors presumably include those which stimulate reproductive activity, and the possible tendencies of birds to return to their natal area or nearby to breed. Therefore ease of dispersal from one island to another, which seems to be indicated by the known immigrations, should not be equated with ease of establishing a breeding population (Grant, 1977). In particular, the absence of magnirostris from Española may have more to do with conditions suitable for starting a breeding population than with dispersal to the island, food supply or competition (see also Abbott, 1978, 1980).

The second area of ignorance is the process of competition over long periods of time. We have shown how annual variation in rainfall alters plant production and produces substantial changes in feeding niches between years (Grant and Grant, 1980b). We have also seen large changes between years in the numerical proportions of conirostris and magnirostris on Genovesa and fortis and scandens on Daphne (Grant and Grant, 1980b). There may have been a fluctuating competitive balance between conirostris and magnirostris on Española, leading to the extinction of the latter perhaps during a series of dry years when Cordia and Prosopis

seeds were rare and conirostris were able to subsist on arthropods found in Opuntia pads and beneath bark. Extinctions are not likely to be observed, but they can be inferred from extrapolations of observed fluctuations. To understand the absence of species on islands and the ecological and morphological differences between those present, there is no real substitute for direct studies of food availability and use by coexisting species over a long period of time (Wiens, 1977; Smith et al., 1978; Abbott, 1980; Grant and Grant, 1980b).

SUMMARY

This study tested predictions of the competition hypothesis which Lack (1945, 1969) applied to Darwin's Finches on the Galápagos islands in order to explain their adaptive radiation. Lack suggested that Geospiza conirostris has competitively excluded G. fortis and G. scandens from I. Espanola and I. Genovesa and G. magnirostris from I. Española; and further that G. conirostris populations exhibit competitive displacement (Genovesa), competitive release (Española), or both. We tested four predictions of this hypothesis using quantitative ecological data and obtained mixed results.

(1) The prediction that Española conirostris has a broad feeding niche which is more similar to a combined magnirostris-fortis-scandens niche than to the niches of these species considered separately was upheld. The niche of Española conirostris is unusually broad.

(2) The prediction that Genovesa conirostris had a feeding niche similar to a combined fortis-scandens niche was not upheld. The niche of Genovesa conirostris is more similar to the niche of scandens alone.

(3) The prediction that conirostris and magnirostris have dissimilar niches on Genovesa, and that the difference lies in magnirostris taking food items exploited by conirostris on Española but not on Genovesa, was verified.

(4) The prediction that conirostris on Española was more efficient than magnirostris at dealing with foods on that island

was not upheld, although *conirostris* on both islands were more efficient than *fortis* and *scandens*.

We conclude that interspecific competition has influenced the distribution and morphology of Darwin's Finches, but our results do not support the hypothesis of competitive exclusion in two particular cases; the exclusion of *fortis* from Genovesa and *magnirostris* from Española by *conirostris*. We cannot explain the absence of *fortis* and *magnirostris* from the two islands by the lack of suitable foods or by the failure of the species to reach these islands. *Geospiza fortis* may be absent because of a combined (diffuse) competitive effect of *magnirostris, conirostris* and *difficilis*. A breeding population of *magnirostris* may be lacking on Española because whenever *magnirostris* arrive, in small numbers, they die, depart or hybridize with *conirostris*. The only condition under which competitive exclusion is likely is the immigration of immature *magnirostris*, because immature birds are likely to be less efficient at dealing with hard seeds than adult resident *conirostris*.

Two areas of ignorance in need of empirical investigation are discussed. The first is the set of conditions that determine the establishment of a breeding population on an island; food supply and competition are not the sole factors. The second is the extent of competition for food in a temporally fluctuating environment.

## ACKNOWLEDGMENTS

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