

## DISTRIBUTIONS OF GALÁPAGOS GROUND FINCHES ALONG AN ALTITUDINAL GRADIENT: THE IMPORTANCE OF FOOD SUPPLY<sup>1</sup>

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**Abstract.** I investigated the abundance, diet and food supply of ground finch species (*Geospiza* Gould) at different altitudes over a calendar year on Isla Pinta, Galápagos. The primary purpose of the study was to evaluate which of three alternative hypotheses best explains the present distributions of species along the vegetation gradient: habitat structure, food supply, or current interspecific competition. Isla Pinta was specifically chosen because Lack (1947) thought that on this island one species, *G. difficilis*, was competitively restricted to the highlands by the morphologically very similar species, *G. fuliginosa*. Four of the five species present were broadly distributed among habitats, and their altitudinal ranges overlapped considerably. The fifth, *G. scandens*, was rare and little was learned of its habits. *G. difficilis* ate mainly litter arthropods and gastropods, especially at high elevations. The remaining three species, *G. fuliginosa*, *G. fortis*, and *G. magnirostris*, were primarily granivorous, but each species consumed a different range of seed sizes. Diet overlap between species was highest when food production was high, and lowest when food was scarce. Seasonal declines in overlap seemed to be mainly due to finches' response to asynchronous food production and a gradual broadening of the available food spectrum. In the dry season the abundance and distribution of the four common species matched to varying degrees the abundance and distribution of the foods they consumed. Effects of current competition on these distributional patterns were not detected. Most *Geospiza* species did not seem to possess strict habitat requirements, and it is unlikely that variation in habitat structure greatly influenced distributions. One possible exception to this is *G. difficilis*, where litter supply may be important. Overall, the data suggest that while competition may be occurring between species, variation in food supply is currently a far more important determinant of distributions on Pinta.

**Key words:** altitudinal distributions; competition; Darwin's finches; diet similarity; Galápagos; *Geospiza*; habitat distributions; population structure.

### INTRODUCTION

The description and interpretation of bird distributions along altitudinal gradients has strongly influenced the way in which ecologists view the distributions of animal species in general (e.g., Mac Arthur 1972). The role of interspecific competition has usually been emphasized, and many of the classical examples of competitive exclusion in nature have been inferred from observed nonoverlapping altitudinal ranges of congeneric bird species on mountains (Diamond 1970, 1975, 1978, Terborgh 1971, Terborgh and Weske 1975).

Patterns of this kind need to be examined more critically; it is not sufficient to make inferences about the action of competition from static distributions alone (Wiens 1977, Simberloff 1978, Grant and Abbott 1980). With respect to altitudinal ranges, alternative models to interspecific competition have occasionally been discussed (e.g., Terborgh 1971), but they have rarely been explored in detail. The food requirements of most bird species are poorly understood. Habitat variation is frequently implicated as a factor but it has not often been quantified, and its relation to food requirements of individual bird species is unknown.

Lack (1947) investigated the distributions of geospizine finches on islands in the Galápagos and judged that interspecific competition for food has been and still is important in producing and maintaining the patterns he reported. From among the several sources of evidence for this view, Lack paid particular attention to the altitudinal separation between the morphologically very similar species *Geospiza difficilis* and *G. fuliginosa* (Fig. 1). *G. difficilis* occurs in the low-elevation habitats only on peripheral islands in the archipelago where *G. fuliginosa* is absent. On the more central islands, where *G. fuliginosa* is ubiquitous at low altitudes, *G. difficilis* is absent or restricted to higher elevation habitats (Lack 1947, based on observations by Snodgrass and Heller 1904 and Gifford 1919). Lack suggested that *G. fuliginosa*, where it had colonized, had outcompeted *G. difficilis* on all but a few islands possessing a highland refuge.

Lack, however, had little information on food resources and he did not carefully consider that differences in habitat requirements might be important (Bowman 1961). I thus undertook a field study designed to examine the hypothesis that competition currently restricts the altitudinal ranges of *G. fuliginosa* and *G. difficilis* on one island where they coexist. I broadened the study to include all *Geospiza* species

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on this island, especially *G. fortis* and *G. magnirostris* (Fig. 1). These might also be expected to compete for food, though less intensely, from Lack's arguments. More generally the study was designed to elucidate the environmental factors that best explain the distributions of *Geospiza* species on this island. Three possible factors are here considered:

- 1) Habitat structure. This hypothesis suggests that the distribution of each species is primarily a result of requirements involving some structural feature in the environment.
- 2) Food supply. This hypothesis explains species patterns mainly on the basis of variation in food supply.
- 3) Interspecific competition. This hypothesis presupposes a role for habitat or food resources, but considers species distributions to be mainly a consequence of current competition between species for these resources.

Hypotheses 1 and 2 assume either that habitat or food resources are not limiting, or that they are limiting but there is little overlap between species in their requirements. Seasonal changes in resource overlap are predicted to result mainly from changes in resource availability. A correlation between finch distributions and either habitat features or food supply is predicted. Furthermore, if these resources are limiting, finch abundance should decline over the period of scarcity.

Current interspecific competition assumes limitation of either food or habitat resources. It also assumes that species overlap significantly in their use of resources, and hence interact through them. The hypothesis predicts specialization in resource use and consequent reduction in overlap between species as resource abundance declines (cf. Smith et al. 1978). It predicts that density of different species should be negatively associated. Note that competition is considered here solely as a significant contemporary process, and not as an historical process that might have led to the evolution of species characteristics.

This report has two purposes. First, I characterize in quantitative terms seasonal and altitudinal variation in finch numbers, food supply, and diets. Second, I use this information to evaluate the importance of the three environmental factors through tests of their assumptions and predictions.

## METHODS

### *Study sites*

Isla Pinta (Abingdon) was chosen for this study because of its accessible highland zone, and relatively undisturbed vegetation (see below). *G. difficilis* and *G. fuliginosa* presently occur together on two other islands, San Salvador and Fernandina. However, the vegetation on San Salvador has been greatly disturbed

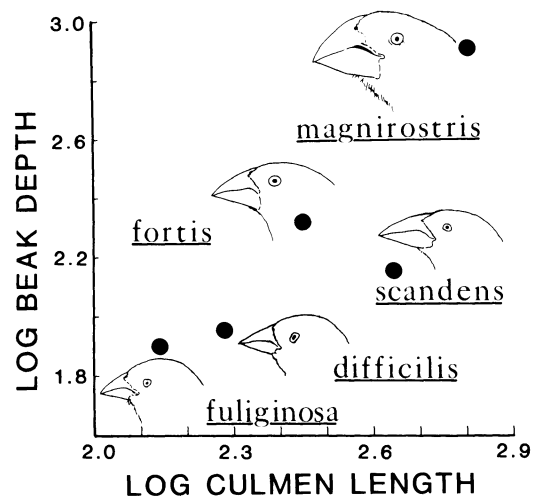


FIG. 1. Mean beak dimensions in millimetres of adult *Geospiza* on Isla Pinta. Characteristics of beak are generally considered to be among the aspects of morphology most closely associated with feeding skills and diet (Bowman 1961, Abbott et al. 1977, Schluter 1982). *G. fuliginosa* and *G. difficilis* are morphologically the most similar species, and Lack suggested that they were the strongest competitors for food.

by goats (Hamann 1981), and there are logistic difficulties in working on Fernandina. Pinta is somewhat isolated, situated to the north of the central cluster formed by Isabela, Santa Cruz, and San Salvador (see Abbott et al. 1977). While quite small (60 km<sup>2</sup> in area; Wiggins and Porter 1971) Pinta has a maximum altitude of 650 m (Adersen 1976) and possesses a highland zone of vegetation similar in appearance to that of several larger islands (e.g., Islas San Salvador and Santa Cruz; Wiggins and Porter 1971, D. Schluter, *personal observation*).

Five 1-ha study sites were established in 1978 on Pinta's southern slope. A sixth was added in 1979. These sites were spaced  $\approx 0.5$  km apart, beginning at 110 m elevation above sea level and extending to 510 m. The sites represent points along the gradient of vegetation change on the southern face of this island. The terminal points of the transect (110 m and 510 m) were situated at the extremes of arid zone and humid forest zone, respectively (Wiggins and Porter 1971).

Feral goats have been present on Pinta since the early 1960's, but eradication programs have significantly reduced their densities and impact on the vegetation. The extent of the damage done by goats was never carefully documented, and it may have been overstated in some qualitative reports (e.g., Eckhardt 1972). Recent work by Hamann (1979, 1981) shows significant regeneration by 1977, and currently the patterns of zonation and plant species composition on the island are quite similar to those prevailing earlier in this century, prior to the introduction of goats (Stewart 1915). Recovery is yet incomplete (Hamann 1979,

1981); for example *Opuntia*, a selectively grazed plant species, is still uncommon on Pinta. It should therefore be realized that the relative abundance of different plants may not now be identical to conditions before 1960.

#### Climate

Climate on the Galápagos is highly seasonal (Wiggins and Porter 1971, Grant and Boag 1980). The wet season, characterized by heavy but infrequent rains, normally extends from late December to May. In the dry season, which lasts for the remaining months of the year, precipitation is more frequent than in the wet, but it falls primarily as a fine mist (*garúa*) and monthly accumulations are relatively slight (Grant and Boag 1980). Precipitation is generally greater at higher elevations year-round. It is the heavier rain of December to May that has the greatest influence on the production of seeds and fruits and on the activity of arthropods (Smith et al. 1978, Grant and Boag 1980, Grant and Grant 1980a). Land birds on the Galápagos typically breed only in the wet season.

#### Dates

Work on Pinta was carried out over a 5-mo period in 1978, and over a full calendar year in 1979. In the 1st yr I visited Pinta on two occasions, the first during the finches' breeding season (6 January–2 April) and the second during postbreeding activity (10–29 May). In 1979 I visited Pinta four times for periods of 5–6 wk. These visits corresponded to early wet season and the onset of breeding (20 January–28 February), late wet/early dry season (26 April–29 May), and middle (9 August–15 September) and late (28 October–3 December) dry season. For convenience, I refer hereafter to 1979 dates as February, May, August, and November.

In 1978 detailed study of diets was restricted to two species, *G. fuliginosa* and *G. difficilis*. Little quantitative information was gained on seed supply, and the study was not continued into the dry season. For these reasons data from 1978 are used only as a supplement, where appropriate, to the more extensive data obtained in the following year.

#### Finch abundance

Five species of ground finches are present on Pinta: *Geospiza fuliginosa*, *G. fortis*, *G. magnirostris*, *G. difficilis*, and *G. scandens* (Fig. 1). Densities of each were determined during every visit to the island, as follows. In 1978 and the first visit of 1979, two mist nets (fixed location) of 12 m length were unfurled at 0700 on each of two successive mornings in each study site. These remained open for 2.1 h in total on each morning, and the number of finches caught was recorded. The number of nets was increased to three for the remaining three periods of 1979. In August of that year persistent rains prevented the opening of nets in the mornings,

and the afternoon period of 1500–1700 was used instead. Finches display similar levels of activity during morning and afternoon periods. I weighed all netted birds and banded them individually or marked them by placing a small notch in a wing primary. Beak and body dimensions were obtained from a sample of adults of each species. Further details of this procedure may be found in Abbott et al. (1977).

I employed a second method of estimating finch abundance in August and November of 1979. On census walks each finch encountered within 10 m to the front or sides of the observer was recorded. This narrow visual field ensured detection of virtually all finches encountered. By walking predetermined, nonoverlapping transects, I covered the entire site exactly once in each census. Five to 11 such walks were conducted per site in each month. Since I obtained information on the diets of finches at the same time (see below), each census required approximately 2–3 h.

For four of the five finch species, the mean number of individuals encountered per hour for a given site and visit was correlated with the total number netted ( $r = .67$ , *G. fuliginosa*;  $r = .75$ , *G. fortis*;  $r = .89$ , *G. magnirostris*;  $r = .64$ , *G. difficilis*;  $N = 12$ ,  $P < .05$ ). Within species, trends for August and November of 1979 do not differ, indicating that afternoon netting results are comparable to morning data. For the fifth species, *G. scandens*, too few individuals were netted or counted for comparison.

A direct count of territories gave a third estimate of *G. fuliginosa* and *G. difficilis* abundance. In February of both years territories of individual males were mapped, and the fraction of each territory that was included in the bounds of the study site was determined. These fractions were summed to yield estimates of breeding density in that area.

#### Finch diets

I used a procedure similar to that of Abbott et al. (1977) and Smith et al. (1978). I quantified diets by systematically walking through study sites and recording with a stopwatch time spent feeding on particular food types, up to a maximum of 5 min per bird. These finches may be approached closely, and on Pinta food items are identified without difficulty. It is therefore unlikely that differential observability of food types biased the diet proportions recorded.

Feeding observation walks were conducted in the mornings and afternoons from 0630 to 1130 and 1500 to 1730. Routes were chosen so that each 10 × 10 m subsection of the site could be scanned at least once by the observer during a morning or afternoon walk. In practice, sites were covered 1.5–2 times in such an interval. Specific routes were altered on a daily basis. I spent 7–11 mornings or afternoons in each site during each 5–6 wk visit.

With the exception of *G. difficilis*, I present the diets of only adult birds for the wet season (February and

May). This is done to minimize effects of a possible bias: young juveniles of all species tended to be much less efficient at handling certain seeds than adults, and young birds frequently interrupted or modified their behavior in the presence of an observer. For *G. difficilis* it was necessary to include juvenile data in order to present diet information for low-altitude sites where adults were uncommon (see below). For this species there was no indication that adult diet was different from that of juveniles in sites where both age groups were present. Adults of all species could be distinguished from juveniles in the wet season by color of beak and gape (cf. Swarth 1929). In the dry season (August and November) I could not easily distinguish adults from immature birds for all five species, either by plumage, beak coloration, or general feeding efficiency, and I therefore include all feeding data in the analysis.

#### *Habitat and food supply*

I examined vegetation and substrate features, and estimated the densities of seeds and ground invertebrates in all four 1979 visits as follows. Sampling quadrats of 1 m<sup>2</sup> were selected using a random numbers table. During each visit I collected 25 random samples from each study site excepting the first (110 m). In the first site I obtained 25 samples in the first visit and 50 thereafter. The doubling in sampling intensity in site 1 was to estimate abundance more accurately for the higher diversity of seed types there. This was necessary for a second study conducted at the same time, on determinants of seed choice (Schluter 1982). I could not sample the remaining sites with the same intensity because of time restrictions.

Within each quadrat the total number of seeds and fruits on the vegetation was counted, and the percent cover of each plant species was assessed by eye. In addition, two subquadrats of 0.125 m<sup>2</sup> were located and the total number of seeds on bare rock surfaces was counted in each. All litter and surface soil (to a depth of 2.5 cm) in subquadrats was collected by hand and transferred to labelled bags. I later (within 24 h) sifted through these on an enamel tray, counting all seeds discovered. I identified arthropods to order, measured their length, and placed them in ethanol-filled vials. In August and November of 1979 I also collected gastropods from litter samples. Volume of the litter portion was determined before samples were discarded. Dimensions (Abbott et al. 1977) of seeds and fruits, and oven-dried masses of these and litter invertebrate samples were determined in 1980.

#### RESULTS

Altitudinal and habitat distributions of finches and food supply have not previously been documented for any Galápagos island. In addition, my quantitative data differ in important respects from the summary reports on distributions by Lack (1947). I therefore begin by

presenting a descriptive account of habitat characteristics and finch abundance patterns in sites on Pinta. This is followed by a description of diets and food availability. Later this information is used to test which of the three hypotheses best accounts for finch distributions.

#### DESCRIPTION

##### *Habitats*

Composition of common plant species on Pinta changes visibly with elevation (Tables 1, 2), and low- and high-altitude sites bear little resemblance to each other in this respect. Differences in structural features among sites include a general increase in the abundance of ground cover and volume of litter with elevation (Table 2). The substrate of site 1 (the arid zone of Lack 1947) is largely bare rock; this contrasts with the deep litter present in the highlands. Tree cover is lowest in the arid zone (site 1), intermediate in the transition zone (sites 2–5), and highest in site 6, the humid zone, where *Zanthoxylum fagara* and other tree species form a nearly closed canopy (Table 2). Shrub density changes irregularly with altitude, and is greatest at low and high elevations. Some seasonal variation in habitat aspects was observed. Lower altitude sites changed most noticeably due to the loss of leaves by *Bursersa graveolens* trees and a reduction in the cover of herbaceous plants in the dry season. However, the rank order of sites by any one structural feature was essentially maintained year-round.

##### *Distributions*

Lack (1947), relying mainly upon the observations of previous visitors to the Galápagos (e.g., Gifford 1919), wrote that the breeding ranges of *G. fuliginosa* and *G. difficilis* were distinct, with *G. difficilis* confined to the humid zone. In fact this is not the case on Pinta, as the distribution of territorial males indicates (Table 3). Territory density of *G. fuliginosa* in February was high and relatively constant through low-altitude sites, but the species was uncommon in site 6, the humid forest zone (Table 3). *G. difficilis*, on the other hand, bred primarily at higher elevations including the *Zanthoxylum* forest (site 6), and was absent from the arid zone (site 1). In both years, *G. difficilis* reached its maximum breeding density at site 5, or below the humid forest zone (Table 3).

Similar data are provided by the February 1979 netting results (Fig. 2). Nonbreeding individuals of *G. fuliginosa* moving through midelevation sites inflated the relative densities there above that shown for breeding birds. Nonetheless the wet season distributions of *G. difficilis* and *G. fuliginosa* overlap and extend over a wide range of elevations.

Breeding densities of two of the three remaining *Geospiza* species are shown in Fig. 2. Netting totals from February 1979 show that, while *G. fortis* was confined

TABLE 1. Common plant species (&gt;5% cover) in Pinta study sites. Site 1 is the lowest in altitude, site 6 the highest.

Species	Sites					
	1	2	3	4	5	6
Trees (>2 m)						
<i>Bursera graveolens</i>	xxx	xxx	xxx			
<i>Pisonia floribunda</i>		xxx	xxx	xxx		xxx
<i>Zanthoxylum fagara</i>				xxx	xxx	xxx
<i>Solanum erianthum</i>						xxx
<i>Croton scouleri</i>						xxx
Shrubs (1–2 m)						
<i>Castela galapageia</i>	xxx					
<i>Lantana peduncularis</i>		xxx				
<i>Waltheria ovata</i>		xxx				
<i>Scalesia incisa</i>		xxx				
<i>Darwiniothamnus tenuifolius</i>				xxx		
<i>Tournefortia rufo-sericia</i>						xxx
Ground cover (<1 m)						
<i>Chamaesyce punctulata</i>	xxx					
<i>Alternanthera filifolia</i>		xxx	xxx	xxx		
<i>Rynchosia minima</i>	xxx*	xxx	xxx	xxx	xxx	
<i>Paspalum galapageia</i>		xxx	xxx	xxx	xxx	
<i>Setaria setosa</i>			xxx*			
<i>Justicia galapagana</i>				xxx†	xxx	xxx
Ferns‡						xxx

\* Wet season only (February–May).

† In August only.

‡ Frequently taller than 1 m.

to the lower three sites, *G. magnirostris* occurred at all altitudes at comparable densities. These results coincide with 1978 data and with my own qualitative impressions (e.g., I have never encountered an adult *G. fortis* in site 4 or higher in the breeding season). Densities of *G. scandens* are not indicated in Fig. 2 because this species was rare in all sites. Occasional observations and net captures indicate that *G. scandens*, like *G. fortis*, breeds exclusively at lower altitudes.

As Bowman (1961) suspected, *G. difficilis* becomes more common in the arid zone after breeding (Fig. 2). In May the altitudinal pattern of this species was almost the reverse of that in February and later in the

dry season. Exactly the same switch was witnessed in 1978. Distributions of the remaining three species also changed in the dry season, and *G. fuliginosa*, *G. fortis*, and *G. magnirostris* became much more abundant in the highlands. Nevertheless, *G. difficilis* was the species most frequently encountered in the humid forest (site 6) throughout the year; all other ground finches apparently avoided this area (Fig. 2).

#### Population structure

By May of 1979 the breeding season was near completion, and a substantial recruitment of juveniles had occurred in most species. This is shown by the increase in the proportion of brown-plumaged birds in their populations between February and May (Fig. 3) and by the increased capture rate of birds in May com-

TABLE 2. Habitat features of sites on Isla Pinta. Mean percent cover of plant categories is an average over four sampling dates of the summed percent covers of individual plant species. The categories Trees, Shrubs, and Ground cover refer to the height of plants: &gt;2 m, 1–2 m, &lt;1 m, respectively.

Site	Altitude (m)	No. angio-sperm species	Mean percent cover			Mean litter volume (L/m <sup>2</sup> )
			Trees	Shrubs	Ground cover	
1	110	38	15.4	20.8	26.0	2.0
2	180	33	39.0	31.9	32.6	2.3
3	225	36	31.8	14.9	47.3	4.9
4	285	32	27.2	11.9	65.8	6.8
5	400	20	36.0	6.8	77.1	10.0
6	510	24	78.6	26.2	64.4	8.3

TABLE 3. Territory density (no./1 ha site) of *Geospiza fuliginosa* and *G. difficilis* in February. No data were obtained from site 4 in 1978.

Site	Altitude (m)	No. territories in site			
		<i>G. fuliginosa</i>		<i>G. difficilis</i>	
		1978	1979	1978	1979
1	110	6.7	6.6	0.0	0.0
2	180	5.3	7.5	0.3	0.0
3	225	6.6	8.0	2.3	1.8
4	285	...	7.9	...	2.7
5	400	5.8	5.4	9.0	6.9
6	510	0.0	0.2	2.3	3.9

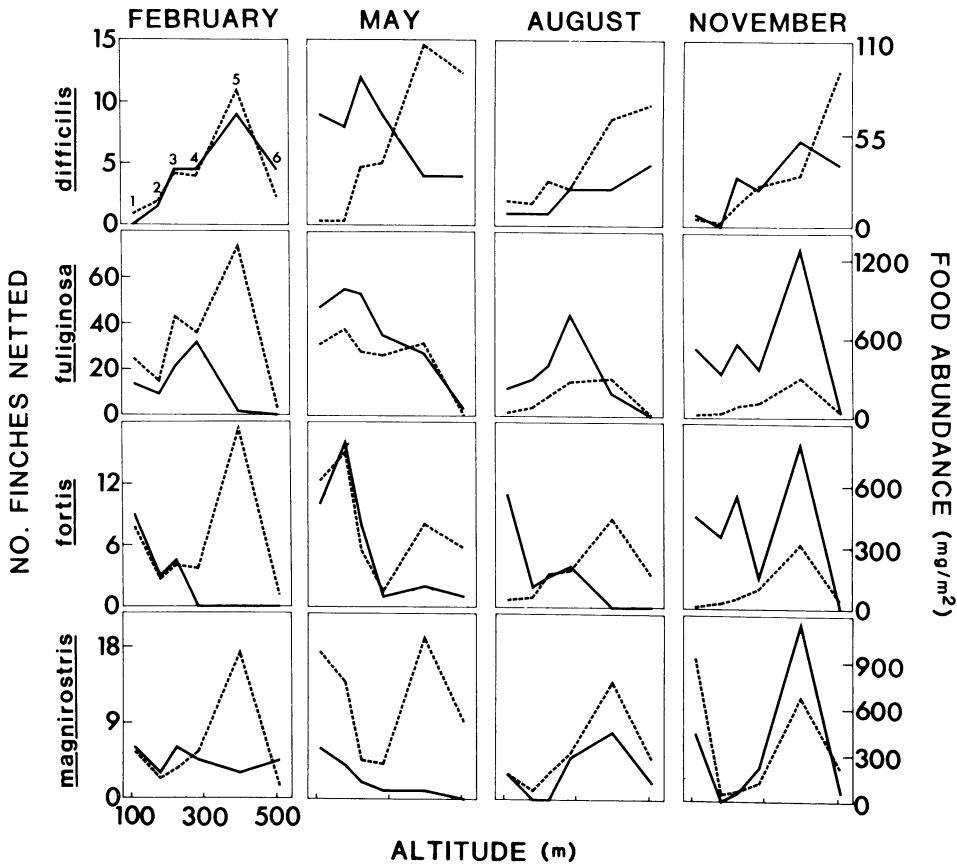


FIG. 2. Finch densities (solid line) and preferred food supply (dashed line) at six altitudes in 1979. Preferred foods are litter arthropods for *G. difficilis*, and seeds for the remaining three species (See Appendix).

pared with February (Fig. 2). Many birds were still feeding fledged young in April and early May. In addition, a rainfall sometime in April resulted in numerous pairs of *G. fuliginosa*, *G. fortis*, and *G. magnirostris* attempting to breed late in this month. The attempt was short lived, however, and I did not record a single successful brood in May.

Distributions of adults of all species were actually quite similar in February and May. Observations of banded adults indicate that this was largely a consequence of birds remaining on or near their territories, possibly to take advantage of potential breeding opportunities late in the season. As a result, shifts in the distributions of species that took place between February and May can be attributed largely to the movement of immature birds. This difference between adult and juvenile distributions was most striking for *G. difficilis* (Table 4). Adults of this species did not attempt to breed in May or later in the year, but banded males were consistently sighted on or near their breeding territories throughout the dry season. Netting records plus observations on individually banded finches show that only immature birds moved to lower elevations in May (Fig. 2). In 1978 the pattern was identical (Table 4), though the difference could not be statistically ver-

ified. The reason why juveniles of this species seem to avoid the highlands is not clear. Possibly they are aggressively excluded from adult home ranges, but I have no observations of this. Slightly different distri-

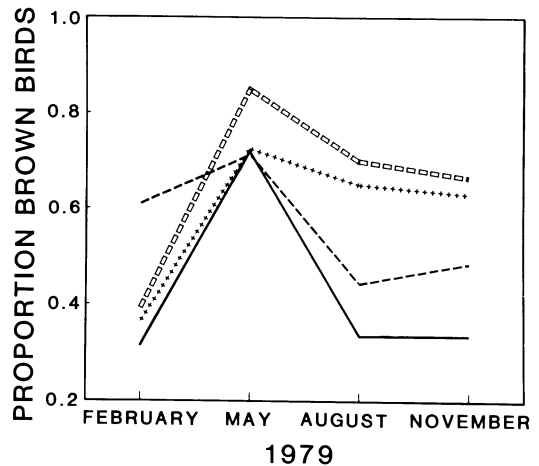


FIG. 3. Proportions of brown-plumaged birds (females and juveniles) in the combined netted samples. Species are *Geosilza fuliginosa* (□□□), *G. difficilis* (—), *G. fortis* (++++), and *G. magnirostris* (----).

TABLE 4. Number of juvenile birds netted per adult in May of 1978 and 1979 for *Geospiza difficilis* and *G. fuliginosa*. No data were obtained in site 4 in 1978. *P* values give the probabilities that adults and juveniles are not differently distributed among sites (chi-square contingency test,  $df = 5$ ). Adult captures were too low to use the test in 1978.

Site	Juvenile : adult ratio			
	<i>G. difficilis</i>		<i>G. fuliginosa</i>	
	1978	1979	1978	1979
1	6.0:1	3.5:1	4.8:1	1.5:1
2	6.0:1	3.0:1	4.8:1	2.1:1
3	15.0:1	5.0:1	5.0:1	4.9:1
4	...	0.5:1	...	2.9:1
5	0.0:1	0.3:1	7.0:1	1.1:1
6	1.0:1	0.0:1	1.0:0	2.0:1
...		<i>P</i> = .01	...	<i>P</i> = .10

butions for adults and juveniles may have been present also in *G. fuliginosa* in May (Table 4), but no trend with altitude was observed.

Breeding had long ceased by August, and uphill shifts by *G. fuliginosa*, *G. fortis*, and *G. magnirostris* included adult birds as well as females and immatures; black- (adult males) and brown-plumaged birds (adult females and young birds of both sexes) did not differ significantly in their distributions (chi-square contingency test,  $P > .10$ ). Flocking was conspicuous in the dry season in these three species, especially at higher elevations. Groups of *G. fortis* or *G. magnirostris* (5–25 birds) were often encountered with the much larger flocks of *G. fuliginosa* (20–200 birds). Small groups of brown *G. difficilis* were often seen in the lower sites throughout the dry season. However, adult males of this species were never found in flocks.

Postbreeding densities of most finches in the six sites exhibited an overall decline between May and August (Fig. 2). Associated with this trend was a decrease in the proportion of brown-plumaged individuals in all populations (Fig. 3). It has been noted elsewhere in the Galápagos, with individually banded finches, that dry season survivorship of brown birds (females and juveniles) is lower than that of adult males (Grant and Grant 1980a, Boag 1981). This explains the trend in Fig. 3 and suggests that reduced postbreeding capture totals for most species (Fig. 2) can be attributed to deaths particularly of juveniles. Indeed, if the relative probabilities of mortality for males and brown birds is reasonably constant through the dry season, then the proportion of brown birds in a sample may serve as an index of total population size. This assumes that juvenile males do not moult from brown to a blackish plumage in the course of the dry season. The assumption is probably valid: Snow (1966) reported that juvenile finches at Bahía Academia began to moult in October or November, but I found no evidence of this on Pinta in 1979. Fig. 3 indicates sharpest reductions

in total numbers between May and August, especially in *G. difficilis*, with slight mortality thereafter.

Increases in the total number of finches netted between successive dry season census dates (Fig. 2) may indicate a real density increase of birds in study sites. However, the activity level of individuals is also a factor, and high November totals may represent the increased catchability of birds at this time (cf. Smith et al. 1978). Observations suggest that this factor influenced both the netting and census walk results.

#### Finch diets

Diets of the four most common species are shown in Table 5 for site 1 in 1979. *G. difficilis* was primarily insectivorous there, though seeds contributed significantly to its diet, especially early in the dry season. Individuals essentially confined their feeding activity to the litter, kicking the surface material backward and seizing items with their beaks. The species was rarely seen removing items from the more extensive rock substrate, and above-ground foods such as pollen and nectar were ignored. The behavior was similar at other sites, and similar in the 2 yr. Most available types of litter arthropods were eaten, though in the breeding season soft-bodied prey such as crickets, caterpillars, and pupae predominated in the diet. In the dry season the principal prey of *G. difficilis* in the highlands was snails encountered in the litter and occasionally on the vegetation.

In contrast *G. fuliginosa*, *G. fortis*, and *G. magnirostris* were primarily granivorous throughout the year (Table 5). Arthropods, primarily caterpillars, were important only in the wet season, and these were taken entirely from the vegetation. Other foods such as pollen, nectar, and berries or arils were also exploited when available (Table 5). The three species consumed seeds from the vegetation, bare ground, and occasionally litter, and were therefore not as restricted in their movements as *G. difficilis*. However, though they fed in the same environment, *G. magnirostris*, the largest species, selected the largest available seeds; *G. fortis* consumed intermediate sizes; and *G. fuliginosa*, the smallest species, ate only the smallest seeds (Fig. 4; see also Schluter 1982).

Table 6 summarizes the similarities in feeding between the four most similar species pairs. For the *G. fuliginosa*-*G. difficilis* comparison, values were computed using small seeds, arthropods, and alternate foods, with the first two categories divided further by microhabitat (litter, open ground, and vegetation). Diet categories for *G. fuliginosa*-*G. fortis*-*G. magnirostris* comparisons are based on types of seeds, fruits, nectar, and pollen without reference to foraging position.

The diet of *G. scandens* was not well quantified due to the scarcity of the species. However of 11 feeding observations, 9 involved *Opuntia*, including flowers, extrafloral nectaries on leaf pads, fruits, and dipteran larvae from rotting leaves.

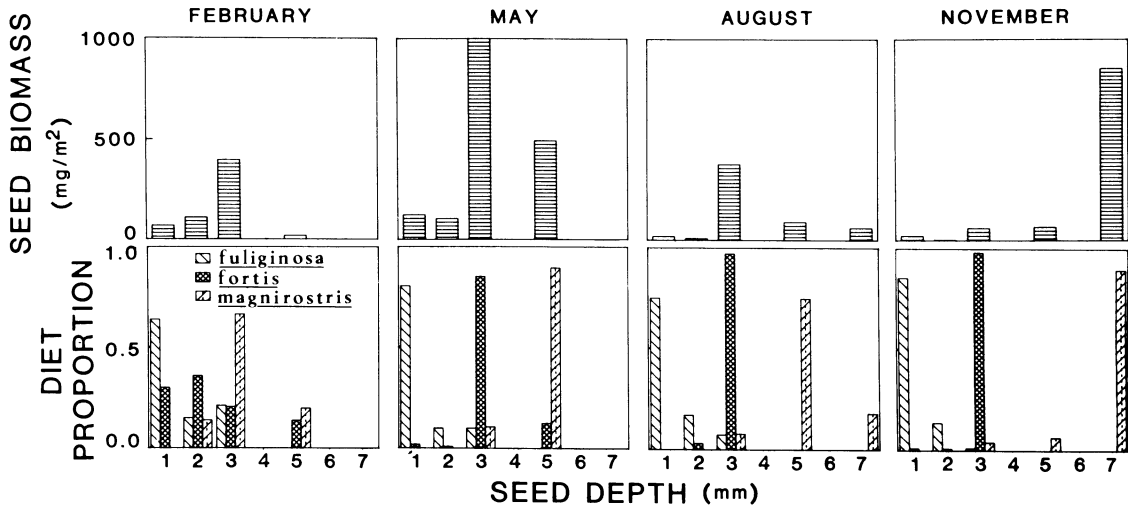


FIG. 4. Use and availability of seeds of various depths by granivore species in site 1. Seed depth is the intermediate of the three orthogonal dimensions: length, depth, and width.

*Food supply*

To evaluate the role of food supply, food abundance must be determined separately for each finch species. I used only those foods which were concentrated upon by the species in question (hereafter called preferred foods). Litter invertebrates are clearly exploited in this way by *G. difficilis* (see earlier, and Table 5). For the granivores *G. fuliginosa*, *G. fortis*, and *G. magnirostris* I used the Abbott et al. (1977) definition of preference: preferred seeds are those whose proportional representation in the diet exceeded 1.5 times their proportion in the environment. This value permits the inclusion of all seeds common in the diet, but excludes certain very abundant foods which are taken only in-

frequently. However, I included only seeds which were preferred (by the 1.5× criterion) in at least 20% of the sites or months in which they were available, in order to exclude foods which passed the 1.5 threshold only sporadically and with no apparent pattern. Subsequent conclusions are not greatly affected by slight variation in these criteria. For example, the 20% criterion excludes ripe *Rynchosia minima* seeds for *G. fortis*. If this food is included, the food supply of *G. fortis* is increased in all sites, but seasonal and altitudinal patterns in food abundance are not changed. The list of seeds satisfying the above criteria for the three granivore species is provided in the Appendix.

Description of food supply as defined here and the

TABLE 5. Finch diets in site 1 in 1979. Values are the proportions of feeding time that the species allocated towards each food type. Months are 2 (February), 5 (May), 8 (August), and 11 (November). Values on the right give the total number of birds observed and seconds of feeding obtained in the particular month.

Species	Month	Diet proportions					Total feeding observed (s)	Total no. birds
		Arthropods	Seeds	Berries arils	Nectar	Pollen		
<i>Geospiza difficilis</i>	2	.92	.08	...	...	...	1780	6
	5	.68	.32	...	...	...	2575	13
	8	.48	.52	...	...	...	6890	29
	11	.88	.12	...	...	...	6820	17
<i>G. fuliginosa</i>	2	.33	.47	...	.13	.01	8770	47
	5	.14	.71	.10	.05	...	15170	78
	8	.06	.92	.01	.01	...	25365	106
	11	.05	.77	.01	.17	...	25430	96
<i>G. fortis</i>	2	.34	.60	.05	.01	.01	2515	16
	5	.15	.76	.07	.02	...	8100	39
	8	.01	.97	.02	...	...	7380	60
	11	...	.96	.03	...	...	7430	31
<i>G. magnirostris</i>	2	.09	.61	.05	...	.24	1970	9
	5	.01	.96	.03	...	...	7820	30
	8	...	1.00	...	...	...	5320	25
	11	...	1.00	...	...	...	9400	37



TABLE 6. Feeding similarity between the four most similar species pairs in sites 1-5 (1979). Values computed using Whittaker's index,  $S = 1 - (1/2)\sum |p(x_i) - p(y_i)|$ . In site 6 and where dashes indicate, diet information was inadequate for comparison (<1500 s total observations for one species of the pair). Months as in Table 5.

Species pair	Month	Study site				
		1	2	3	4	5
Feeding similarity, S						
<i>Geospiza fuliginosa</i> and <i>G. difficilis</i>	2	.15	.30	.21	.19	.23
	5	.08	.15	.03	.02	.03
	8	.05	.03	.00	.00	.01
	11	.01	.12	.01	.02	.04
<i>G. fuliginosa</i> and <i>G. fortis</i>	2	.45	.58	.67	...	...
	5	.20	.23	.34	...	...
	8	.08	.18	...	...	.12
<i>G. fortis</i> and <i>G. magnirostris</i>	2	.44	.48	...	...	...
	5	.25	.55	.15	...	...
	8	.08	...	...	...	.19
<i>G. fuliginosa</i> and <i>G. magnirostris</i>	2	.25	.22	...	.31	.04
	5	.04	.11	.05	.11	.01
	8	.01	...	.00	...	.07
	11	.05	...	...	.00	.25

use of this variable in tests requires an important assumption: it is assumed that abundance of preferred foods adequately represents abundance of foods available to a species. Preference is treated as a given species characteristic. Results of an earlier study (Schluter 1982) support this assumption (see also Discussion).

Biomass of litter arthropods generally increased with elevation in all seasons (Fig. 2), though in February densities peaked in site 5. The data are not shown, but exactly the same pattern was observed in February 1978. I collected snails from the litter in the dry season and litter seeds in both seasons, though the abundance of these is not illustrated in Fig. 2. The relation between *G. difficilis* prey and altitude is unaltered by this omission.

Seed densities were quite variable among months, and overall reductions between February and November are evident in the food supply of *G. fuliginosa* and *G. fortis* (Fig. 2). The foods of *G. magnirostris* remained abundant throughout the year, particularly in sites 5 and 1. Excepting May, the quantity of preferred seeds of *G. fuliginosa* and *G. fortis* was generally most abundant in site 5. The humid forest habitat (site 6) was consistently low in density of seeds of all types.

Differences among sites in food abundance for the four species in Fig. 2 were significant in all months (Kruskal-Wallis,  $P < .01$  in all cases).

TESTS

*Distribution and abundance*

The habitat structure hypothesis predicts a correlation between finch density and the abundance of

TABLE 7. Correlations between finch density and litter volume (*Geospiza difficilis* only) and food supply (all species). Coefficients in parentheses are based on finch density obtained from census walk data; other values are from netting results. Underlined coefficients are significant at the 95% level.  $N = 6$  in each case.

Species	Correlation with finch density			
	February	May	August	November
Litter volume				
<i>G. difficilis</i>	<u>.93</u>	-.67	.72 (.75)	<u>.93</u> (.72)
Food availability				
<i>G. difficilis</i>	<u>.92</u>	-.75	<u>.84</u> (.93)	.57 (.92)
<i>G. fuliginosa</i>	.08	<u>.85</u>	<u>.58</u> (.92)	<u>.88</u> (.79)
<i>G. fortis</i>	-.01	<u>.94</u>	-.06 (-.11)	.62 (.36)
<i>G. magnirostris</i>	-.41	.46	<u>.91</u> (.92)	.71 (.94)

habitat features exploited by that species. For most species, however, there was little indication that their distributions were associated with any specific habitat variable. The exception is *G. difficilis*, which confined its feeding activity to the litter. Except in May, the density of this species was positively correlated with litter volume (Table 7). Despite small sample sizes, two of these correlations are significant. Some support for the habitat structure hypothesis is thus provided in this one case.

The food supply hypothesis predicts a positive statistical association between finch density and the abundance of foods. For *G. difficilis* this was the case in three of four sampling periods (Table 7): finch density and litter arthropod abundance covaried in all months but May. However, food abundance and litter volume tended to share the same distribution (Table 2 and Fig. 2), making it difficult to separate statistically the effects of each variable on *G. difficilis* distribution. None of the partial correlations is significant ( $P > .05$ ), but power is low since only three degrees of freedom are provided in each test. I therefore pooled dry season data (August and November) and repeated the analysis. Of four partial correlations, only one is significant ( $P < .01$ ), that between *G. difficilis* density (census walk results) and arthropod abundance, holding the effects of litter volume fixed. The same test was not significant when netting results were used instead of census walk results ( $P > .05$ ). Thus, while some suggestion is given that food supply might be more important than habitat structure, further sampling is necessary to verify this.

Densities of the remaining three finch species were not well correlated with seed supplies in February. This corresponds to a time when the finches were breeding, and when the proportion of seeds in the diet was lowest (Table 5). In May, seeds constituted a much greater portion of the diets, and for *G. fuliginosa* and

*G. fortis*, altitudinal variation in netting totals are largely explained statistically by variation in the supply of seeds (Fig. 2 and Table 7). Thereafter, a strong positive relationship between finch density and food supply was present in *G. fuliginosa* and *G. magnirostris*, and to a lesser extent in *G. fortis* in November. These results agree with expectation, and support the food supply hypothesis. However, throughout the dry season the numbers of *G. fuliginosa* and, especially, *G. fortis* in the lower sites was greater than expected from the abundance of their seeds (Fig. 2).

The competition hypothesis predicts that the densities of different species should be negatively associated along the altitudinal gradient. I therefore searched for competitive effects by examining the degree of statistical independence of distributions. The most similar species in diet are the granivores, *G. fuliginosa*, *G. fortis*, and *G. magnirostris* (Table 6). In the dry season, when food was relatively scarce, abundance of these three species covaried to a large extent (Fig. 2), ruling out obvious negative effects among them. An interpretation of this is that their foods were similarly distributed. Nonetheless, there might have been some form of competitive compensation in the densities of the three species. This hypothesis predicts that when one species is more abundant than expected from its food supply, the other species should be, on average, less abundant. I tested this by first regressing density of each species (netting results) onto food abundance for the combined months of August and November. A regression is justified since both a dependent and an independent variable can be specified (Snedecor and Cochran 1967). Because both variables are subject to measurement error the regression model will tend to underestimate the true regression coefficient (see also Ricker 1973). This bias does not critically affect the present analysis.

Two of the regressions are significant (*G. fuliginosa*,  $r = .63$ ,  $P = .03$ ; *G. fortis*,  $r = .49$ ,  $P = .11$ ; *G. magnirostris*,  $r = .73$ ,  $P = .008$ ;  $N = 12$  in each case). Standardized residuals from the three regressions were then summed across species for each of the 12 cases. If residuals for each species are independent then the variance of these 12 values should be approximately equal to the sum of the variances of the standardized residuals, 3 in this example. In this case the population variance of the 12 sums (hereafter called  $\chi^2$ ) will be chi-square distributed with 12 degrees of freedom. For *G. fuliginosa*, *G. fortis*, and *G. magnirostris* the value for  $\chi^2$  (23.9) falls above the 95% critical range for chi-square (two-tailed test; Rohlf and Sokal 1969). The competition hypothesis is not supported, since  $\chi^2$  was significantly larger than the expectation from the null hypothesis (12): when one finch species was more abundant than predicted from its food supply, one or both of the other two species was also more abundant than expected.

For *G. fuliginosa* and *G. difficilis* the result is sim-

ilar. In this case  $\chi^2$  is also  $>12$  ( $\chi^2 = 18.2$ ), but not significantly so ( $P > .05$ ). I repeated both tests using census walk data instead of net captures to estimate finch abundance. For the three granivores the result was essentially the same ( $\chi^2 = 21.0$ ,  $P = .10$ ). For *G. difficilis* and *G. fuliginosa*,  $\chi^2$  was below expectation under the null hypothesis ( $\chi^2 = 7.15$ ), indicating a possible slight negative interaction between them. However, the result is not significant ( $P > .10$ ). Finch distributions, therefore, do not appear to be negatively associated. Indeed, in three of four tests the opposite trend was detected. The prediction of the competition hypothesis is thus not strongly supported by these data.

If food limits population size, finch abundance is predicted to decline over the period of food scarcity. Fig. 2 shows that food supply of most species declined most sharply between May and August in all sites. The same figure and Fig. 3 indicate sharpest declines in finch numbers and greatest mortality of brown-plumaged birds over this same period. This parallel decrease provides some suggestion that food might have been limiting in the dry season.

#### Diet overlap and seasonality

The food supply hypothesis predicts that species should differ in feeding position and food type, if foods are limiting. The observation of such differences thus lends support to the food supply argument (see earlier). However, there is overlap between species as required by the competition argument (Table 6). The relation between this overlap and food supply may be used to distinguish between the hypotheses.

The food supply hypothesis predicts that diet overlap should reflect variation in food availability. There is some evidence for this. Fig. 4 illustrates the dynamics of variation in the utilization of seeds of different sizes in site 1 for the three granivores. Rains triggered the production of seeds in January and February. Plants yielding smaller seeds were the first to respond, and all three species consumed the newly available resource (Fig. 4). Larger seeds, especially *Bursera graveolens*, appeared in abundance in May, and *G. fortis* and *G. magnirostris* responded by shifting their efforts to these. Diet overlap declined correspondingly (Table 6). The largest available food, *Castela galapageia*, did not appear before August, and this seed was very abundant in November. In response, *G. magnirostris* further altered its behavior such that its diet consisted almost solely of this large seed. In other sites the shifts were similar: one of the few resources important in the diet of all three granivores was the soft green *Rynchosia minima* fruit. In the dry season, diet overlap between them was highest during periodic bursts in the production of this fruit (e.g., site 5 in November; Table 6). The fruit matures quickly into a hard seed, and all three finch species switched to other foods when this occurred.

*G. difficilis* behavior was also sensitive to nonuni-

form shifts in resource levels. Diet overlap between this species and *G. fuliginosa* (Table 6) was high when the typically ground-feeding *G. difficilis* ate seeds off the vegetation. However, this happened only when the seeds were first produced in abundance at the beginning of the wet season. By May many seeds had fallen to the ground, and *G. difficilis* had switched accordingly. Diet overlap declined as a consequence.

Competition might also have influenced variation in diet overlap. An earlier study (Schluter 1982) has shown that feeding behavior of granivorous finches is best understood by assuming that each food type occurs in a distinct patch type. In this situation, if a species affects the abundance of foods consumed by other species, then in time diet overlap between them should decline (MacArthur and Pianka 1966, Smith et al. 1978). Hence if resource competition was occurring on Pinta we would expect diet similarity to have decreased as food supply diminished. This was often the case. For example, at low altitudes the major decline in food supply of most finches occurred between May and August (Fig. 2), and diet similarity declined over the same interval (Table 6).

However, the data suggest that competition was less influential than food supply in effecting seasonal changes in resource overlap. First, the competition hypothesis does not explain diet overlap early in the year. In the lowlands the initial large decline in diet similarity occurred between February and May (Table 6). As food availability actually increased over this period (Fig. 2), it is unlikely that competition had had a significant effect. Second, if food competition was primarily responsible for the next major decline in similarity (between May and August; Table 6) then this decline should have resulted from greater diet specialization. Table 8 lists diet breadth of all three granivorous species in site 1. Values indicate that diet breadths of all three species were stable through the dry season, and over the period May to August there were no substantial declines. Diet similarity therefore appears to have decreased over this period as a result of species separating more widely over the food spectrum. This separation corresponds to asynchronous production of different foods resulting in a broader food spectrum in the dry season (Fig. 4), and agrees with the prediction from the food supply hypothesis.

#### DISCUSSION

Much impetus for the debate concerning the importance of interspecific competition in nature derives from the basic question: what type of evidence is needed to show that this factor is the causal one in any specific example? Researchers have occasionally considered the appearance of particular forms of community structure to be evidence of competition's importance, but many now agree that more rigorous rejection of alternative hypotheses is required (Colwell and Fuentes 1975, Connell 1975, 1980, Wiens 1977, Simberloff 1978,

TABLE 8. Diet diversity ( $H' = -\sum p_i \ln(p_i)$ ) for the three granivorous species in site 1, 1979.

Month	<i>Geospiza fuliginosa</i>	<i>G. fortis</i>	<i>G. magnirostris</i>
February	2.1	1.9	1.3
May	2.3	1.2	0.5
August	2.2	1.2	0.8
November	2.0	1.0	0.6

Grant and Abbott 1980). In this study I tested the hypothesis that interspecific competition is the major cause of finch distributional patterns along an altitudinal gradient in Galápagos. Data from an analysis of resource use and availability are most consistent with an hypothesis that food supply is currently of greater significance than either competition or habitat structure in determining these patterns.

Various observations suggest the primacy of food supply. First, all species were broadly distributed over a range of habitat types. Distributions of most species varied from one season to the next, but I was unable to identify any structural component of habitat that varied in unison. In addition most species were apparently unspecialized in feeding position and also breeding behavior (e.g., nest site placement; see Lack 1947). There was therefore little evidence to suggest that any habitat requirements could not be met equally well in all sites. The exception is *G. difficilis*, which obtained most of its food from the litter. Over most of the year the abundance of this species was correlated with litter volume, and so for this species habitat structure may be important on its own. However, since its distribution was also correlated with food abundance (Table 7), it is difficult to distinguish between the food supply and habitat structure hypotheses in this one case.

Second, the diet of each finch species on this island differed substantially from the diets of other species. Diet overlap between species was present nonetheless, but it was high only when food was abundant. Similarity was highest early in the wet season when finches were least abundant and when food production was greatest. Overlap in diet decreased through the dry season in most sites, but this seemed to be due to irregular changes in the abundance of foods not obviously related to their removal by consumption. Finches did not become greatly specialized in their use of food types as supply diminished. Instead, diet breadth was quite constant, and overlap declined when species switched to different feeding positions or food types. This corresponded to changes in the availability of food types mainly as a result of asynchronous food production.

Third, the abundance of most species in the dry season was positively correlated with the availability of its foods. Moreover, changes in the relative densities of foods in study sites were matched by shifts in the

distributions of finches. Negative associations among potential competitors were not detected, even when the distribution and abundance of their foods were considered in the analysis. Interspecific territoriality and other forms of aggression between species were not observed.

Finally, some evidence suggests that foods were limiting in this system. Total finch abundance increased and declined seasonally, together with the biomass of foods available. Mortality in populations of all species was greatest over the period of time when food supply decreased most dramatically (May to August). In addition, the species whose May distribution least matched the distribution of foods available (*G. difficilis*) suffered the greatest relative losses in this interval.

These results and conclusions do not argue for the absence of interspecific competition for food in this system. Rather, they suggest that factors other than competition, mainly variations in the food supply itself, are far more important in determining altitudinal distributions and other attributes of finch populations. Terborgh (1971) and Terborgh and Weske (1975) have also considered this possibility, and they included climatic and vegetational features in addition to interspecific competition as proximate causes of avian distributional limits on Peruvian mountains. However, the data presented here show that more subtle factors may determine bird distributions along such gradients.

Two assumptions of the test procedure require some discussion. The first supposes that foods available to each species are adequately characterized by those foods upon which they concentrate. It is assumed that competition does not presently affect their choice or preference. A detailed study of seed choice on Pinta (Schluter 1982) provides some justification for this. First, seed size is correlated with seed hardness (Abbott et al. 1977) and the range of seed sizes used tend to be those which can be successfully handled. This range is determined by beak size (see also Grant et al. 1976, Abbott et al. 1977, Grant 1981). Second, within the range of seed sizes consumed, finches spent a disproportionate amount of time on those seeds providing the highest biomass returns per unit time spent foraging. Third, diet breadth relative to availability of different foods did not change greatly with season (Schluter 1982). These data indicate that diet was closely related to feeding skills and morphology, and hence food choice may be considered as approximately 'given,' and not influenced by competition, at least over the short term.

Some indication of limited flexibility in feeding behavior was observed in this study. In May when *G. difficilis* became quite abundant in lowland sites (Fig. 2) its feeding position remained remarkably similar there to that of individuals in the highlands, despite the very low abundance of litter and litter foods. An interesting possibility is that this restricted and unique

behavior is itself a result of evolution in a more competitive past environment. A test of such an hypothesis is beyond the scope of this study.

A second assumption is that all food items within the range consumed are equally important in determining finch abundance. However, finches might be particularly responsive to changes in the density of a few seed types. One possible example is *Cenchrus platyacanthus* which occurred only in the low-altitude sites on Pinta. In site 1 when this seed was available, the proportion of *G. fortis*'s diet made up of *C. platyacanthus* was 32–365 times the proportion in which the seeds occurred in the habitat. This extraordinary preference might indicate a particularly valuable seed to *G. fortis*, and might explain the greater-than-expected abundance of this finch in lowland sites (Fig. 2). Abundance of nonseed diet components may have influenced distributions similarly. For example, nectar supplies are variable among sites, and are greatest at low altitudes. The relatively high density of *G. fuliginosa* in these low sites (Fig. 2) suggests that the species may have responded to nectar availability as well as to seeds.

These conclusions concerning the importance of food complement those of some previous authors. Bowman (1961) studied the diets of several ground finch populations in Galápagos and was the first to counter Lack's (1947) view that competition may be prevalent. However, his basic premise was that, while overlap in diets existed, food supply (which he did not measure) might not be limiting. More recently, Wiens and Rotenberry (1979) reached a similar conclusion in their study of diets of breeding grassland and shrubsteppe birds. The evidence for unlimited supplies of foods in their system was strong (see also Rotenberry 1980) but their study was restricted mainly to the breeding season. In contrast, while there is some indication that on Pinta food was indeed limiting in the dry season, the effects of resource variation predominated nonetheless.

Other researchers in the Galápagos have argued more strongly for the effect of competition on diet (Smith et al. 1978). My conclusions are different from theirs possibly because diet overlap was greater in the late, wet season of their study than in mine (see also Abbott et al. 1977), or because the effects of nonuniform production of foods were less pronounced. They also restricted their study to arid-zone sites where food production was often considerably less than on Pinta, particularly in the dry season. These authors did not estimate the importance of changes in relative food availability on diet changes (Smith et al. 1978). Nevertheless, there is a real possibility that the different results reflect island-to-island variation in the intensity of food competition.

Another variable which may account for different conclusions regarding competition is annual food production level. Considerable year-to-year variation in rainfall has been documented for the Galápagos (Grant

and Boag 1980), and substantial differences in food availability in dry seasons of different years have been observed (Grant and Grant 1980*b*). Pulliam and Brand (1975) and Pulliam and Parker (1979) have shown similar annual variation in seed production in continental areas. Unfortunately, I do not have information on annual differences in rainfall or food availability for Pinta. On Isla Santa Cruz, 1979 rainfall at a site on the southern coast was recorded at 229.6 mm (Estacion Cientifica Charles Darwin, *personal communication*). This figure is somewhat lower than the mean for 1965 to 1980 ( $384 \pm 57.3$  mm SE) and is nearly half of the 1978 figure (417.1 mm). Moreover, on Pinta, densities and distributions for all finch species were extremely similar in February and May of the 2 yr (e.g., Table 3, 4). Feeding behavior of *G. difficilis* and *G. fuliginosa* also did not differ noticeably between years. These data suggest that 1979 was not an unusual year, though it might have been drier than average. Nonetheless, more data would be required to evaluate the significance of annual variation to tests of the three hypotheses. It is possible that food production on Pinta is frequently much lower than in 1979, in which case the effects of interspecific competition for food on distributions may be more detectable.

Effects of food supply on population sizes of ground finches have been noted elsewhere in the Galápagos (Smith et al. 1978, Grant and Grant 1980*b*). However, no comparable data exist concerning the relative importance of resource supply and competition on distributions of sympatric populations of these birds. Of course, the effect of food supply on bird distributions has been appreciated in other avian systems (e.g., Wiens and Johnston 1977, Pulliam and Parker 1979).

#### CONCLUSION

In conclusion, altitudinal distributions of ground finches on Pinta seem to be mainly a result of variation in the supplies of their largely different sets of foods. Seasonal shifts in finch distributions can also be attributed to this variable, and habitat structure seems not to play a role in most cases. Food may limit population sizes in the dry season. Diet overlap between species was low, especially when food was scarce, and was highly sensitive to changes in the abundance of different foods through irregular production and other processes not obviously related to interspecific competition. Interspecific competition may be present in this system, but the process did not seem greatly to influence altitudinal distributions.

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APPENDIX

Preferred seeds of the three granivore species on Pinta. Seed depth refers to the intermediate of the three orthogonal dimensions: length, depth, and width (Abbott et al. 1977). Preference is defined in the text.

Plant species	Seed depth (mm)	<i>Geospiza fuliginosa</i>	<i>G. fortis</i>	<i>G. magnirostris</i>
<i>Darwiniothamnus tenuifolius</i>	.29	+		
<i>Aristida repens</i>	.33	+		
<i>Trichoneura lindleyana</i>	.35	+		
<i>Bouteloua disticha</i>	.47	+		
<i>Chamaesyce punctulata</i>	.48	+		
<i>Cyperus andersonii</i>	.57	+		
<i>Portulaca</i> sp.	.63	+		
<i>Alternanthera filifolia</i>	.73	+		
<i>Acalypha sericea</i>	.73	+		
<i>Setaria setosa</i>	.74	+		
<i>Polygala galapageia</i>	.80	+		
<i>Salvia occidentalis</i>	1.00	+		
<i>Paspalum galapageia</i>	1.01	+		
<i>Boerhaavia caribaea</i>	1.08	+	+	+
<i>Alternanthera echinocephala</i>	1.00	+		
<i>Scalesia incisa</i>	1.24	+		
<i>Commelina diffusa</i>	1.47	+	+	+
<i>Heliotropium angiospermum</i>	1.51	+	+	+
<i>Cenchrus platyacanthus</i>	2.11		+	+
<i>Lantana peduncularis</i>	2.15		+	
<i>Rynchosia minima</i> *	2.45	+	+	+
<i>Croton scouleri</i>	2.85			+
<i>Tournefortia rufo-sericea</i>	3.65			+
<i>Zanthoxylum fagara</i>	4.03			+
<i>Bursera graveolens</i>	4.16		+	+
<i>Opuntia galapageia</i>	4.58			+
<i>Castela galapageia</i>	6.59			+

\* Green fruit.