

## Annual Variation in Finch Numbers, Foraging and Food Supply on Isla Daphne Major, Galápagos

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**Summary.** (1) We report some effects of an annually variable and unpredictable rainfall upon Darwin's Finches on the Galápagos. Finch numbers, foraging and food supply were studied on I. Daphne Major in December of 1973 and 1977, and compared. 1973 was the second of two successive wet years and 1977 was a drought year.

(2) Seed numbers and biomass were approximately one order of magnitude lower in the drought year than in the wet year. Small and soft seeds were absolutely and relatively rarer in the drought year than in the wet year.

(3) Similarly finch numbers and biomass were approximately one order of magnitude lower in the drought year than in the wet year. Numbers of *G. scandens* declined less than did number of *G. fortis*. Both species exhibited unbalanced sex ratios, in favour of males, in the dry year in contrast to balanced sex ratios in the wet year. Male *scandens* were heavier on average in the wet year, but male *fortis* were heavier in the dry year.

(4) The foraging of *scandens*, a cactus (*Opuntia*) specialist, was similar in the two years. The foraging of *fortis* in the dry year differed from foraging in the wet year in three important respects: *fortis* devoted a disproportionate amount of time to feeding on small seeds while tending to avoid seeds of *Opuntia*, they fed more on floral and extra-floral parts of *Opuntia* and they fed on *Tribulus cistoides*, a large and hard fruit which was absent from their diet in the wet year. As a consequence of feeding more on *Opuntia*, *fortis* foraging was more similar to *scandens* foraging in the dry year than in the wet year.

(5) The results are discussed in relation to expectations from competition theory. The decline in numbers in relation to a decline in food supply was expected, but a convergence in diets was not. The convergence is attributed to the recent renewal of a single resource, *Opuntia* flowers, against a background of general resource scarcity. Diet overlap and limitation of numbers by food provide indirect evidence of interspecific competition; *scandens*, with an included niche, was competitively superior to *fortis*.

proach to direct manipulation is to document the responses of consumers to seasonal reductions in food.

Adopting this approach, Smith et al. (1978) compared the food supply, foraging and numbers of Darwin's Finches on four Galápagos Islands at contrasting wet and dry seasons. The results were largely consistent with expectations from competition theory. From wet to dry season finch numbers and food supply declined at two sites, but at two others finch numbers remained high where food supply remained plentiful. Total finch biomass was correlated with food abundance at five dry season sites but not at eight wet season study sites. As food became scarce, diets of sympatric species diverged and diet overlap diminished. Smith et al. (1978) suggested that variation in the intensity of competition among islands in the archipelago is enhanced by year to year difference in food supply caused by the unpredictable Galápagos rainfall. This leads to the expectation that food supply and finch numbers are depressed particularly severely during years of little or no rainfall, partly as a consequence of interspecific competition for food (Smith et al., 1978). A second expectation is that diet overlaps are minimal at the end of a dry year because diets diverge following the depletion of those resources jointly exploited by competitor species (see also Colwell and Futuyma 1971, Hurlbert 1978, Lack 1947).

In 1977 we were able to test these expectations. During the wet season, January to May, only 25 mm of rain fell on one of our study sites, I. Daphne Major. Only one finch species, *Geospiza scandens*, bred, and none of the offspring survived more than four months (P.T. Boag, pers. comm.). The contrast with 1973, the year of our first study (Abbott et al. 1977; Grant et al. 1975; Smith et al. 1978), could scarcely be greater. 1972 had been an exceptionally wet year, owing to the occurrence of an 'El Niño' phenomenon (Houvenaghel 1974; Wyrski et al. 1976) and unusually heavy rains persisted into the early part of 1973 in the archipelago. In 1973, two or more clutches were produced by both of the resident species on Daphne, *G. scandens* and *G. fortis*, and survival of the offspring of both was greater than 80 per cent over an eight month period. Both species bred in the years 1974–1976 and densities stayed quite high until the rains failed in 1977. We therefore returned to Daphne in December 1977 and repeated our 1973 study procedures.

There are no comparable studies from Galápagos. Annual variation in finch numbers and food supply has been largely a matter for speculation (Lack 1947). The most similar study to ours was conducted by Morel and Morel (1974) in the African Sahel. A one order of magnitude reduction in dove numbers was associated with a drought, but no quantitative estimates of food and feeding were made.

### Introduction

Interspecific competition for food has been frequently invoked to account for patterns of resource partitioning among closely related species in natural communities (Cody 1974; MacArthur 1972; Pianka 1976; Schoener 1974a). Experimental investigation of the process of competition has been difficult to pursue except in highly simplified segments of communities. An alternative ap-

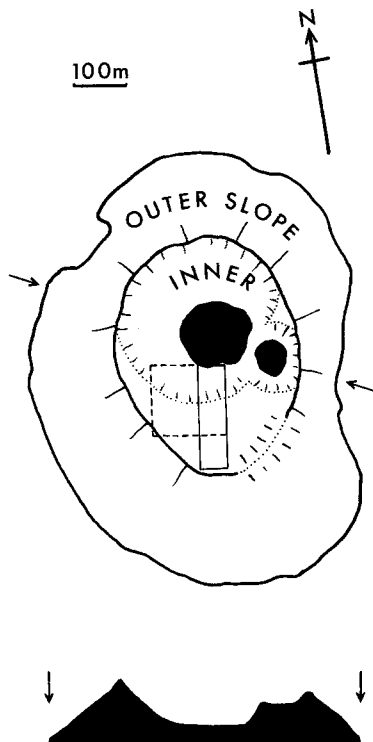


Fig. 1. Map of I. Daphne Major, showing the study area used in 1973 (broken line) and 1977 (solid line). The two craters are shown in black

## Methods

Daphne Major (Fig. 1) has a circumscribed area of 32 ha (Wiggins and Porter, 1971). In view of the steep terrain, the superficial area is likely to be close to 40 ha (Grant et al. 1975). The altitude, determined separately by altimeter and by triangulation in 1975, is approximately 120 m. The island lies approximately in the centre of the archipelago, 8 km north of the much larger Isla Santa Cruz and the same distance west of Isla Baltra.

We stayed on Daphne from 23 November 1977 to 5 January 1978, but conducted all censuses and measurements reported here in the same period as in 1973, i.e., 6–16 December. We have used mist-netting and Lincoln Index estimation of finch population sizes in our Galápagos studies before because the lack of territoriality of most of the birds outside the breeding season, the mobility of the birds and their silence preclude the standard bird censusing techniques of registering territorial males (see Abbott et al. 1977, Grant et al. 1975, Smith et al. 1978). To census birds this time we operated mist nets at the same positions and times of day as before. However, we used 12 m nets for 16.5 h instead of 9 m nets for 22 h; both give a total of 198 net-m-hrs. To test for a bias in capture rates associated with net length we recorded the position, to the nearest metre, of all birds captured in a similar programme on this island in June–July 1975, grouped the captures in  $6 \times 2$  m intervals from centre to ends and tested the null hypothesis of uniform distribution of captures by  $\chi^2$ . The result is  $\chi^2_3 = 1.23$ ,  $P > 0.9$  for  $N$  captures = 209. Therefore netting results were unaffected by net length when the adjustment for time is made. However the adjustment for time is a little problematical as there is usually a slight tendency for capture rates to decline during the approximately two or three hours the nets are open. Therefore our use of long nets for a short time tends to bias our capture

rates upwards; as will be seen in the comparison with 1973, this is a conservative bias.

Birds were weighed to the nearest 0.1 g with a Pesola spring balance and missing colour bands (if any) were replaced before the bird was released. We adhered to a system of individually marking birds that was initiated by P.T. Boag and ourselves in 1975; one numbered, metal, leg band and three colored, plastic (Darvik), leg bands were used. More than 50 per cent of the finches alive in 1977 were banded in 1975–1977. Using these recognition marks, we estimated population numbers by applying the Lincoln Index method to observational data obtained along the same census routes used in 1973 (Grant et al. 1975).

To characterize finch foraging, we made daily records of foraging activities with a stop watch in a study area of approximately 23,000 m<sup>2</sup> (Abbott et al. 1977). As in 1973, a lower limit of 5 s and an upper limit of 300 s per bird per day was set.

To estimate seed density and plant phenology state, we used a random number method for obtaining 33 quadrats of 1 m<sup>2</sup> in the eastern half (20 m  $\times$  50 m) of the study area (Fig. 1). In 1973 the whole grid had been sampled 50 times. The reason for the change in method is that time was needed to sample the outer slope in continuation of a programme started in 1975. It was justified by the fact that in each of the 1973 samplings the two halves of the grid had yielded similar results, and a 10% accuracy in the sampling (Southwood 1966) of all the common seed species was achieved in less than half of the 50 quadrats. Numbers of fruits and seeds attached to each plant species in the whole 1 m<sup>2</sup> quadrat were counted and recorded. To these were added 8 times the number of fruits and seeds found on the ground in a 0.125 m<sup>2</sup> area of the quadrat, thus giving a total seed and fruit density (numbers/m<sup>2</sup>). Seed size, volume and hardness of all the species have been determined before (Abbott et al. 1977; Smith et al. 1978). We assumed no year to year changes occurred in hardness and size of seeds and fruits. This assumption was tested with fruits of *Tribulus cistoides* and found to be correct.

## Results

### Vegetation

Table 1 shows a comparison of the frequency of occurrence and reproduction of plants in the two years. Two species, *Bursera malacophylla* and *Portulaca howelli*, were recorded more frequently in 1977 than in 1973. Since *B. malacophylla* is a slow growing tree, its increase probably resulted from the alteration in the sampling programme (Methods) and not from an actual increase in plant abundance. The same may be true of *P. howelli*, which is a slow-growing perennial herb. Most of the other species were recorded less frequently in 1977 than in 1973. Three species, *Heliotropium angiospermum*, *Coldenia galapagoa* and *Ipomoea linearifolia* were not recorded at all in 1977. The reduction in occurrence of these plants is a real phenomenon and not attributable to a change in the sampling programme. All species were present in both years but the three species just mentioned were extremely rare in 1977, both in the sampled and non-sampled halves of the grid, as determined by inspection.

Reproductive activity of the plants was very low in 1977 (Table 1). This too was a general condition and not just restricted to the sampled area, for a thorough search of the part of the grid not sampled failed to locate a single flowering or fruiting stem of *Herissantia crispa*, *Heliotropium angiospermum*, *Coldenia galapagoa* and *Ipomoea linearifolia*.

**Table 1.** Frequency of occurrence of vegetation in randomly chosen 1 m<sup>2</sup> quadrats: for 1973 N=50 quadrats, for 1977 N=33 quadrats. Figures for buds, flowers and fruits are totals for the 50 quadrats in 1973, and totals in 1977 adjusted to 50 quadrats

	1973				1977			
	Percent Occurrence	Buds	Flowers	Fruits	Percent Occurrence	Buds	Flowers	Fruits
<i>Opuntia echios</i> Howell	20	87	20	168	18	35	4	11
<i>Bursera malacophylla</i> Robins	34	0	0	0	45	0	0	0
<i>Croton scouleri</i> Hook. f.	2	0	0	0	3	0	0	0
<i>Herissantia crispa</i> (L.) Brizicky	26	0	2	73	6	0	0	0
<i>Portulaca howelli</i> (Legr.) Eliass.	26	0	0	0	48	0	0	0
<i>Chamaesyce</i> spp. <sup>a</sup>	16	300	380	247	3	18	24	6
<i>Tribulus cistoides</i> L.	20	1	0	0	3	0	0	0
<i>Heliotropium angiospermum</i> Murr.	34	122	173	391	0	0	0	0
<i>Coldenia galapagoa</i> Howell	22	0	0	187, 100	0	0	0	0
<i>Ipomoea linearifolia</i> Hook. f.	10	0	0	8	0	0	0	0

<sup>a</sup> Includes *C. amplexicaulis* (Hook. f.) Burch and *C. punctulata* (Anderss.) Burch

Outside the study area, two recognizable cactus clumps situated at the north-west side of the small crater were examined in both years. Bush 1 had a bud: flower: fruit count of 263:47:460 in 1973 and 53:2:63 in 1977. Bush 2 had a count of 349:39:350 in 1973 and 130:21:352 in 1977. Thus but for fruits on bush 2, production was greater in 1973 than 1977. This complements the results from samples in the study area.

### Seed Density

Table 2 compares the density of seeds on plants and on the ground in the two years. The overall density is one order of magnitude lower in 1977 than in 1973. Seed abundance in 1977 was only

**Table 2.** Seed density. Mean and one standard error for 1 m<sup>2</sup> quadrats are shown

	1973	1977
<i>Portulaca howelli</i> (Legr.) Eliass.	0.2	7.5 ± 2.9
<i>Eragrostis cilianensis</i> (All.) Lutati	5.3 ± 3.6	1.9
<i>Coldenia galapagoa</i> Howell	3724.0 ± 1209.4	1.0
<i>Heliotropium angiospermum</i> Murr.	10.8 ± 6.9	0
<i>Chamaesyce</i> spp. <sup>c</sup>	60.0 ± 45.7	9.0 ± 5.6
<i>Herissantia crispa</i> (L.) Brizicky	120.8 ± 23.1	0
<i>Opuntia echios</i> Howell <sup>a</sup>	660.5 ± 339.5	50.4 ± 32.4
<i>Ipomoea linearifolia</i> Hook. f.	15.0 ± 10.2	37.1 ± 12.4
<i>Cenchrus platyacanthus</i> Anderss.	1.6	0
<i>Merremia aegyptica</i> (L.) Urban	44.6 ± 9.3	52.7 ± 12.3
<i>Tribulus cistoides</i> L. <sup>b</sup>	80.5 ± 22.8	92.1 ± 34.3
<i>Cacabus miersii</i> (Hook. f.) Wettst.	96.9 ± 56.3	18.4 ± 13.6
<i>Acalypha parvula</i> Hook. f.	1.6 ± 0.8	0
<i>Amaranthus sclerantoides</i> Anderss. (Anderss.)	0	26.4 ± 9.4
Total numbers per m <sup>2</sup> <sup>b</sup>	4821.8 ± 1212.9	295.5 ± 48.5
Total volume (cm <sup>3</sup> ) per m <sup>2</sup> <sup>b</sup>	14.9	5.2

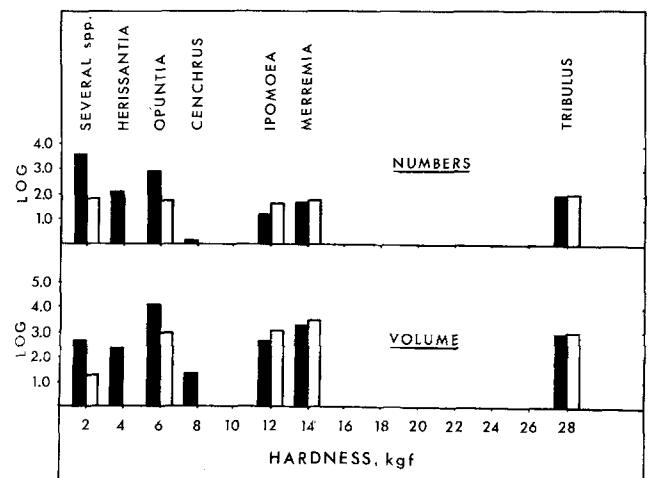
<sup>a</sup> Composed of a mixture of fruits and seeds. To convert fruit numbers to seed numbers the empirically determined 82 seeds/fruit was used.

<sup>b</sup> Number of fruits, since seeds are never found by themselves. There are 3-5 (av. 4) seeds/fruit.

<sup>c</sup> *Chamaesyce amplexicaulis* (Hook. f.) Burch and *C. punctulata* (Anderss.) Burch fruits (3 seeds/fruit). Fruits, rather than seeds, are listed, because fruits are eaten whole by the finches.

6 per cent of what it was in 1973. Seed biomass, as estimated crudely by total volume (seed coat plus kernel; see Smith et al. 1978), differed by less. The 1977 volume was 35% of the 1973 volume. However, if the seeds of *Merremia aegyptica* and *Ipomoea linearifolia* are eliminated from the comparison because they are not eaten by finches (see below), the 1977 volume (1.6 cm<sup>3</sup>/m<sup>2</sup>) is only 13% of the 1973 volume (12.3 cm<sup>3</sup>/m<sup>2</sup>).

The most conspicuous contrast between the years is in the density of some small seeds. *Heliotropium angiospermum*, *Coldenia galapagoa* and *Herissantia crispa* were moderately common to abundant in 1973 but rare or absent in 1977. Several other species show a trend in the same direction but the confidence limits on the estimates of density are broad and overlapping. The broad confidence limits arise from the patchy distribution of the seeds. All species with a density of seeds greater than 5/m<sup>2</sup> were tested by Morisita's index of dispersion, I<sub>d</sub>, and all were found to be significantly aggregated (P<0.01). Two seed species, *Portulaca howelli* and *Amaranthus sclerantoides*, are exceptions to the trend, being commoner in 1977 than in 1973 (Table 2). In the first, and possibly the second, the difference may be due to a change



**Fig. 2.** The abundance of seeds on *Daphne* in 2 kgf hardness classes in 1973 (solid bars) and 1977 (open bars). Hardness is the force necessary to crack a seed (see Abbott et al. 1977 for details). *Tribulus* hardness varies according to how the fruit is cracked (see text p. 60)

in the grid sampled with a consequent elevation of plant density (Table 1); note that *Amaranthus sclerantoides* is an annual, and plant density could not be estimated in either year.

Figure 2 illustrates the difference in composition of the seed samples. Relatively smaller quantities, both numbers and biomass, of small and soft seeds were present in 1977 than in 1973. Hardness is the only seed property used in the Figure because it is positively correlated with seed depth in the Daphne samples ( $r=0.522$ ,  $df$  14,  $P<0.05$ ), and because a size-hardness index such as the (depth  $\times$  hardness)<sup>1/2</sup> index used by Abbott et al. (1977), gives the same results as does hardness alone.

### Finch Numbers

There were fewer finches in 1977 than in 1973. Our netting results indicate a one order of magnitude difference (Table 3). Our estimates based on a simple application of the Lincoln Index method yield a slightly smaller difference. However, in 1973 there were reasons for believing that the assumption of random dispersal of banded birds throughout the populations was not met. To allow for this we stratified the island (Grant et al. 1975) and in two analyses we combined the estimates from the three strata.

**Table 3.** Finch numbers. Netting totals are from 198 net-metre hours of trapping.  $\times$  indicates present on island. 95 percent confidence limits are given for the Lincoln Index estimates.<sup>1</sup> Model 1 in Grant et al. (1975)

	1973	1977
<i>(1) Netting totals</i>		
<i>G. fortis</i> Gould	93	13
<i>G. scandens</i> (Gould)	43	4
<i>G. magnirostris</i> Gould	13	$\times$
<i>G. fuliginosa</i> Gould	14	$\times$
<i>Camarhynchus psittacula</i> Gould		1
<i>Certhidea olivacea</i> Gould	$\times$	
<i>Dendroica petechia</i> (Gould)	2	$\times$
<i>Zenaida galapagoensis</i> (Gould)	12	1
Total ground finches ( <i>Geospiza</i> species)	163	17
<i>(2) Lincoln Index estimates</i>		
<i>G. fortis</i> Gould	1176 $\pm$ 388 <sup>1</sup>	177 $\pm$ 28
<i>G. scandens</i> (Gould)	286 $\pm$ 128 <sup>1</sup>	109 $\pm$ 16
<i>G. magnirostris</i> Gould	39 $\pm$ 45 <sup>1</sup>	14 $\pm$ 18
<i>G. fuliginosa</i> Gould	139 $\pm$ 151 <sup>1</sup>	$\times$
Total number of ground finches	1640 $\pm$ 712 <sup>1</sup>	300 $\pm$ 62
Total wet weight Biomass of ground finches (kg)	26.43	5.80

This gave estimates, without confidence limits, of total finch numbers in the region of 1975–2100. In other words, the 1973 estimates given in Table 3 are probably too low, and the difference between years is correspondingly greater than shown. It is likely that 1977 numbers were no larger than 15% of 1973 numbers. There was no need to stratify the island in 1977.

Regardless of the exact reduction in overall number, it is clear that both *fortis* and *scandens* had significantly lower populations in 1977 than in 1973. Ninety-five per cent confidence limits do not overlap. The confidence limits are much smaller in 1977 than in 1973 because the proportion of banded birds was much higher in 1977 (64 and 67% for *fortis* and *scandens*) than in 1973 (16 and 20% respectively). Similarly *fuliginosa* numbers must have been reduced in 1977 because throughout our stay, 23 November 1977 to 5 January 1978, we positively identified only four individuals of this species including two which were banded, whereas in 1973 we netted 16. The overall finch density was 27–54/ha in 1973 (Grant et al. 1975) and 6–9/ha in 1977.

The difference between years in overall biomass is smaller than the difference in numbers. There are several contributing factors. It is partly due to the greater relative abundance of the large *magnirostris* in 1977 than in 1973, and to the absolute and relative scarcity of the small *fuliginosa* in 1977. Moreover *scandens*, which is heavier than *fortis*, was relatively more common in 1977 than in 1973 to judge from the Lincoln Index estimates; the netting results indicate the opposite, but the small number of captures in 1977 cannot be reliably used to estimate proportions of species. Numbers of *fortis* declined to 15% of 1973 numbers, but *scandens* declined to only 38%. Finally *fortis* were significantly heavier in 1977 ( $\bar{x} \pm S_x = 17.31 \pm 0.31$  g,  $N=38$ ) than in 1973 ( $15.13 \pm 0.13$  g,  $N=132$ ;  $t_{161}=7.69$ ,  $P<0.001$ ), and *scandens* were marginally heavier on average in 1977 ( $21.12 \pm 0.44$  g,  $N=16$ ) than in 1973 ( $20.12 \pm 0.36$  g,  $N=41$ ;  $t_{54}=1.48$ ,  $P>0.1$ ).

### Population Structure

The age and sex structure of the *fortis* and *scandens* populations was quite different in the two years (Table 4). First, there were no birds in 1977 less than a year old. In contrast a third of the *scandens* population and two thirds of the *fortis* population in 1973 were birds born that year. Second, the sex ratio was unbalanced in 1977 and apparently balanced in 1973. Birds in black plumage are males. Those in brown plumage are either females or else males which have not yet acquired black plumage. Without laparotomizing the brown birds (cf Curio and Kramer 1965) or recording sex-specific behavioral traits such as singing, it is not possible to distinguish males from females in the brown

**Table 4.** Age and plumage characteristics of all banded finches known to be alive in December 1973 and 1977. Adults in black plumage are males, those in brown plumage are either males or females.  $N$  is sample size

Plumage Year	<i>Geospiza fortis</i>				<i>Geospiza scandens</i>			
	$N$	% Adults		% Imma- tures Brown <sup>a</sup>	$N$	% Adults		% Imma- tures Brown <sup>a</sup>
		Black	Brown <sup>a</sup>			Black	Brown <sup>a</sup>	
1973	187	16.6	13.9	69.5	59	28.8	37.3	33.9
1977	109	67.0	33.0	0	64	78.1	21.9	0

<sup>a</sup> The allocation of birds to these two age categories is based upon bill colour, being darker in adults than in immatures, particularly in the upper mandible. The reliability of the method has not been tested

plumage class, hence the uncertainty about the sex ratio. Nevertheless, black-plumaged birds clearly predominated in 1977 among both *fortis* ( $X_1^2=12.56, P<0.001$ ) and *scandens* ( $X_1^2=20.25, P<0.001$ ). The result is duplicated, at the same level of significance, in an analysis of unbanded birds seen on the census, and in an analysis of all birds (banded and unbanded) captured in mist nets. Females may have suffered more than males in breeding (*scandens*) or in the attempt to breed (*fortis*) in this year. In contrast, in 1973 the ratio of black to brown birds (and possibly males to females), did not differ from an expected 1:1 ratio in either adult *fortis* ( $X_1^2=0.44, P>0.1$ ) or adult *scandens* ( $X_1^2=0.64, P>0.1$ ).

Many, possibly a majority, of the birds alive at the end of 1977 were born in or earlier than 1973. Six *fortis* banded in 1973 were known to be alive at the end of 1977; three were banded in 1973 as adults and three as immatures. Five *scandens* banded in 1973 were known to be alive at the end of 1977, all having been banded as adults in 1973. All eleven birds had been recaptured in the period 1975–1977 and given metal and plastic bands in replacement of the more easily removed celluloid bands given in 1973. Since the six *fortis* represent three per cent of the birds banded in 1973, three per cent of the population size in 1973 survived to 1977. Three per cent of 1176 is 38. This figure should be at least doubled to 76, and possible tripled to 114 to correct for band loss from birds banded in 1973 and lacking bands in 1975–1977. By the same procedure we estimate a minimum survival of 1973 *scandens* to be 25. Correcting for band loss, lower in this species than in *fortis* (Grant et al. 1975), we should double this figure to 50. The reliability of these estimates cannot be determined. Even if they are only approximately true, they indicate a low population turnover rate, particularly in *scandens*.

#### Condition of the Finches

Since males are heavier, on average, than females the larger average weights recorded in 1977 may be due to the predominance of males in *fortis* and *scandens* samples. To compare the condition of birds in the two years by means of their weights it is necessary to restrict attention to a single sex class. This can be done unambiguously only with black-plumaged males; such a restriction has the additional advantage of excluding all one-year olds, which may not have reached adult size and weight. Black *scandens* were heavier in 1973 than in 1977 ( $t_{27}=2.25, P<0.05$ ), but black *fortis* were heavier in 1977 than in 1973 ( $t_{42}=3.36, P<0.005$ ).

A difference in average weights between years could be due to either a difference in feeding conditions, and hence physiological condition of the birds, at the time of study, or to differential survival of small and large birds prior to study periods in the two years. To test the second possibility we compared the width of the lower mandible. It was chosen for three reasons. Unlike wing length, the obvious choice as an index of body size, beak width is not seasonally abraded. It has the least measurement error of the several dimensions we have studied (cf Abbott et al. 1977). Also our measurements in 1973 correspond well with measurements of the same birds made by P.T. Boag in 1975–1977. This is important because most of the banded birds alive in 1977 were measured by P.T. Boag. A two per cent discrepancy between measurements by PRG and PTB was corrected before the comparisons were made. For both species there is no significant difference in the lower mandible width in 1973 and 1977 samples of black males; for *fortis*  $t_{90}=0.94, P>0.1$ , and for *scandens*  $t_{63}=1.32, P>0.1$ . Other dimensions (wing length, tarsus length, several bill

**Table 5.** Proportion of the time spent foraging at various locations expressed as percent of total foraging time

	<i>Geospiza fortis</i>		<i>Geospiza scandens</i>	
	1973	1977	1973	1977
<i>Opuntia echios</i>				
Flowers	39.0	38.4	93.3	56.1
Buds	0	2.0	5.3	29.8
Spine base nectaries	0	17.8	0.3	6.0
Pulp from stems	0	1.9	0	5.7
Seeds/fruits on ground	5.0	0.2	1.1	0.2
	44.0	60.3	100.0	97.8
<i>Tribulus cistoides</i>				
Fruits	0	19.5	0	0
Leaves	0	0.4	0	0
	0	19.9	0	0
<i>Chamaesyce</i> spp.				
Fruits	37.6	8.4	0	0
<i>Heliotropium angiospermum</i>				
Fruits	11.1	0	0	0
<i>Coldenia galapagoa</i>				
Seeds	0	1.2	0	0
Small seeds on ground	7.2	10.1	0	2.2
Total seconds	4680	9775	1875	9350
Number of observations	49	88	21	72
Minimum number of birds	38	31	14	25

dimensions) were examined but not tested for significance. They gave no indication of a difference between years. Therefore, weight differences between years appear to reflect differences in physiological condition of the birds rather than differences in body size.

#### Foraging

The predominant feeding activity in both years was the exploitation of several parts of cactus, *Opuntia echios*. At this time of the year, December, *scandens* can be described as an *Opuntia* specialist whereas *fortis* is more of a generalist (Table 5). The difference between years for *scandens* is minor; more time was devoted to flower buds in 1977 than in 1973. This is associated with a lower abundance of flowers in 1977 (Table 1). The difference in flower abundance is greater than the difference in consumer (*scandens*) abundance. The buds opened by *scandens* were ready to open the same day, the peak time of opening being 9:00–10:00 a.m. Their exploitation by *scandens* represents an earlier access to the flower resource than is possible for *fortis*, which is constrained by its bill shape to forage on open flowers.

There are much larger differences between years in the foraging of *fortis*. In 1973 the small fruits and seeds of *Heliotropium angiospermum* and *Chamaesyce* spp. were common (Table 2), and their exploitation accounted for about half of the foraging activity of *fortis*. In 1977 *Heliotropium angiospermum* was virtually absent, and *Chamaesyce* fruits were greatly reduced in abundance and correspondingly were exploited to a relatively small extent. Com-

compensation for the rarity of small seeds and fruits took the form of exploiting the hard and large fruits of *Tribulus cistoides*, and devoting more time to feeding on *Opuntia echios*. The consequence of feeding more on *Opuntia* is a greater similarity with the foraging of *scandens*. In 1973 the similarity was 0.401 by the index of Renkonen (Goodall 1973) and Whittaker (Whittaker 1960), whereas in 1977 it was 0.507. We have chosen this measure of similarity rather than Hurlbert's (1978) measure of niche overlap because it is on a scale of 0 to 1, unlike Hurlbert's unstandardized measure, which is essential for the comparison we make.

The foraging of *fortis* on seeds can be compared with the seed supply. In 1973 the distribution of foraging activity matched closely the abundance of seeds grouped into 2 kgf hardness categories. The similarity between food available and foraging time distributions is 0.891. This arises from a heavy concentration of foraging time (91.8%) on the abundant seeds in the lowest hardness class (80.9%). In 1977 when the abundance of seeds in this class was reduced to 50% of the 1973 value, the similarity between food available and foraging time distributions was reduced to 0.517. A new food item, fruits of *Tribulus cistoides*, was included in the diet.

Two other seed species were not included in the diet in either year. These are *Ipomoea linearifolia* and *Merremia aegyptica*. The average hardnesses of  $10.4 \pm 0.5$  kgf ( $N=20$ ) and  $12.3 \pm 0.6$  kgf ( $N=20$ ) respectively are distinctly lower than the  $27.3 \pm 1.6$  kgf ( $N=20$ ) for *Tribulus cistoides* (Fig. 2). But *fortis* exploits *Tribulus* fruits by a biting and twisting motion that involves less force expended than is registered by our machine (see Abbott et al. 1977) for measuring hardness when it is applied to the fruit in the manner used by *magnirostris*, i.e. in the midline (P.R. Grant, in prep.). Having now observed *fortis* biting at the corners of the fruit we have attempted to duplicate this with the seed cracking machine. The hardness value thereby obtained is  $5.83 \pm 0.86$  kgf ( $N=12$ ). This is less than is necessary for the birds to crack *Ipomoea* and *Merremia* seeds. *Merremia* seeds may not be cracked also because they are globular and cannot be gripped securely in the beak, and both *Merremia* and *Ipomoea* may not be exploited because they are chemically protected. *Merremia* and *Ipomoea* may therefore be unavailable to the finches and the similarities need to be recalculated following their exclusion. When this is done the similarities between available food and foraging time distributions become 0.901 in 1973 and 0.748 in 1977. The lower similarity in 1977 is accounted for by more time spent on seeds in the smallest hardness class and an avoidance of *Opuntia* seeds, most of which were in fruits.

Observations on foraging in other parts of the island generally correspond well with observations made in the study area. In 1973 six *fortis* were observed cracking *Tribulus* fruits outside the study area, but this feeding activity was clearly rare, confined to a few individuals and was not observed in the study area either casually or during the recording of foraging. In both years *fortis* were daily observed gleaning seeds, fish fragments and possibly insects from the nests of Blue-footed boobies, *Sula nebouxii* in the two craters.

## Discussion

In 1973 seed density and volume on Daphne were approximately the same at the end of the wet season in April and at the end of the following dry season in December (Smith et al. 1978). Presumably this was brought about by an approximate balance between seed production and consumption during the interval. It

is known for example that such perennials as *Heliotropium angiospermum*, *Coldenia galapagoa* and *Chamaesyce* spp. flower and fruit in August on Daphne (Tj. de Vries pers. comm. of observations in 1974). The similarity in April and December food supply shows that contrasting seasons do not necessarily have contrasting food conditions. Therefore years of contrasting rainfall may not produce contrasting food conditions. Our expectations about finch numbers and foraging activity in 1977 were conditional upon food supply. If food supply was found to be similar in the two years, we expected finch numbers, finch biomass and foraging activity to be similar. On the other hand, if the drought of 1977 had adversely affected seed production that year, we expected finch numbers and biomass to be lower in 1977 than in 1973.

Our sampling showed that seed density and biomass were indeed lower in 1977 than in 1973. Our first expectation, conditional upon this result, was observed; finch numbers and biomass were much reduced in 1977 compared with 1973. In fact the decline in numbers took place in 1977 through the death, and possibly emigration, of adults and through the failure of both species to reproduce successfully (P.T. Boag, pers. comm.).

The question arises as to whether or not interspecific competition for food leading to starvation contributed to the decline in finch numbers. One indication of competition would be diminished dietary overlap between *fortis* and *scandens* under conditions of food scarcity. This expectation is derived from arguments about competition for food developed by Lack (1947; see also Smith et al., 1978), and is most succinctly stated by Hurlbert (1978, p. 76) "the competitive interactions most influential in determining overlap of realized niches will be those that have taken place prior to the moment of observation. The stronger these interactions are, the smaller the degree of overlap that will be observed, other things being equal."

The expectation of diminished dietary overlap was not observed. Diets had not diverged in 1977 but had converged as a result of a change in foraging activity of *fortis*. But the "other things" referred to by Hurlbert were not equal; the resource spectrum had changed in the few weeks before our observations were made. Most importantly *Opuntia* had started flowering in early October on Daphne in 1977 (R. Tompkins, pers. comm.). By the time our study began, *Opuntia* nectar and pollen were plentiful relative to other resources, and were exploited more than any other resource by both *fortis* and *scandens*. We suggest that the major reason for the observed convergence in diets was the renewal of these *Opuntia* resources against a background of general resource scarcity. If interspecific competition had occurred prior to October, the renewal of *Opuntia* flowers alleviated its effects and prevented us from detecting it by the simple method of comparing diet overlaps in different years.

Other considerations lead us to conclude that interspecific competition for food did occur before October. First, diets of *fortis* and *scandens* overlap in the wet season (Abbott et al. 1977) and in the dry season of a wet year (Smith et al. 1978) and a dry year (this study). Thus the potential for interspecific competition probably exists at all times providing that food is limiting. Second, a reduction in finch numbers in relation to food supply is evidence of food limitation. Food limitation coupled with diet overlap is suggestive evidence of interspecific competition. It does not prove competition because the food resources which are jointly exploited may be irrelevant to the determination of population numbers. However, the feeding niche of *scandens* is included in the feeding niche of *fortis*; all resources exploited by *scandens* are also exploited by *fortis*. Therefore if the *scandens* population is food limited at times, its size is at least partly governed by competition with

*fortis*. We have no evidence for supposing that other biotic agents, such as disease (cf Gifford, 1919) and predation by short-eared owls (Grant et al. 1975), contributed substantially to the decline in population numbers.

The same argument in a slightly different form can be made about *fortis*. Two facts suggest that *fortis* was an inferior competitor to *scandens*: this competitive inequality is characteristic of species with an included niche relationship (Miller 1967). Numbers of *fortis* declined more than numbers of *scandens*, and *fortis* exhibited a diet shift whereas *scandens* did not. In 1977 *fortis* foraged on the fruits of *Tribulus cistoides*, an item which was virtually absent from their diet in 1973. *Tribulus* fruits are large, hard and difficult to crack. Their inclusion in the diets of *fortis* can be accounted for by the low overall seed abundance partly as a result of consumption by *scandens*.

The superior physiological condition in 1977 of *fortis* compared with *scandens*, as judged by weight, supports the hypothesis that *Opuntia* flowering alleviated the effects of food shortage. It can be calculated from Tables 1 and 3 that there were more open *Opuntia* flowers/*fortis* in 1977 than in 1973, but there were fewer open *Opuntia* flowers/*scandens* in 1977 than in 1973. As further evidence that the supply of pollen and nectar for *scandens* was relatively low in 1977, note the greater frequency of bud-opening in 1977 (Table 5), suggesting that open flowers were not numerous enough to meet the daily energy needs of *scandens*. But there remains one anomaly; why were *Tribulus* fruits (and small seeds) retained in the diet of *fortis* in 1977 when *Opuntia* pollen and nectar were relatively plentiful and body weights were high? Possibly a mixed diet is essential to this species (cf. Westoby 1978) or else further exploitation of *Opuntia* was rendered uneconomical by higher rates of interaction with the aggressively dominant *scandens*.

Thus the decline in finch numbers was brought about in part by interspecific competition for food. In seeking to identify the evidence for competition we have failed to emphasize independent responses of the two species to their food supplies. Such non-competitive responses may be much more important than competitive ones. For example, survival of the sexes was similarly unequal in *fortis* and *scandens*, suggesting a common response to deteriorating food conditions that place unequal energetic burdens on males and females (P.T. Boag and P.R. Grant, in prep).

We conclude with three general remarks. First, in studies of competition through niche analysis there is a need to document the process of dietary shifts through time, e.g. at short intervals throughout a period of food stress, rather than relying upon point estimates of diets and diet overlaps under two contrasting conditions. This is evident from the complications arising from resource renewal in the present study, and from the warning (Colwell and Futuyama 1971, Hurlbert 1978) that niche overlap at a single time and interspecific competition cannot be equated. Second, there is a need for replication. Our study was unable to provide these two desiderata, and is limited in consequence. A few studies have been made of seasonal changes in feeding habits of presumed competitor species of vertebrates, and they are subject to the same limitation (see Smith et al. 1978).

Third, we re-iterate the point made by Smith et al. (1978) that current models of optimal diets are inadequate to characterize, and hence predict, the diets of competitor species under conditions of changing resource variety and spatial distribution. Optimization models have been useful in predicting diets in laboratory and simple field situations (Cody 1974, Krebs 1978, Pyke et al. 1977). Our observation of diet expansion by *fortis* is consistent with a prediction of the effect of a competitor species from the compres-

sion hypothesis of MacArthur and Pianka (1966; see also Schoener 1974b). But the conditions of the models that consumers feed in a fine-grained fashion and that resource variety is constant are violated in many situations, such as ours. These restrictions of the models need to be relaxed (e.g. see McNair 1979) so that the models can be used to make unambiguous predictions of diet changes as a result of interspecific competition.

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