

SEED AND PATCH SELECTION BY GALÁPAGOS GROUND FINCHES: RELATION TO FORAGING EFFICIENCY AND FOOD SUPPLY¹

DOLPH SCHLUTER

Division of Biological Sciences, University of Michigan, Ann Arbor, Michigan 48109 USA

Abstract. I investigated the diets of three species of Darwin's ground finches (*Geospiza* Gould) on Isla Pinta, Galápagos. Diet choice was examined in relation to both the finches' handling efficiency on seed types and the profitability of patches. Handling efficiency on different seed types was related to the size of the finch species. Correspondingly, the two larger finch species generally ignored small seeds with low rewards, and the two smaller finches avoided feeding on seeds apparently too large and hard to crack. In *G. fuliginosa*, the smallest species, seed choice was correlated with seed depth within the range of seed sizes actually consumed. In addition, the proportion of its diet made up of given seed types was correlated with the profitability of patches within which these seeds occurred. Certain seed types providing low individual returns per unit handling time were highly profitable by virtue of their high density within patches. Conversely, large search times between valuable seeds diminished the relative profitability of respective patch types. Diet breadth of *G. fuliginosa* was investigated in relation to seasonal changes in food supply. Results on seed choice in relation to relative densities of seed types were ambiguous, but a slight shift toward feeding on smaller seeds in the dry season was detected. However, the shift could be explained by the greater profitability of patches of the small seeds in this season. These finches did not generalize their use of patch types, despite a large seasonal decline in food abundance. This result contradicts a prediction of optimal foraging theory. Several possible explanations for this are discussed, including an hypothesis that when food was abundant finches selected a diet that was less than maximally efficient.

Key words: *Darwin's finches; diet breadth; Galápagos; Geospiza spp.; optimal foraging; patch selection; profitability; seasonal differences; seed selection.*

INTRODUCTION

Considerable theoretical and experimental research is presently focused on the optimal choice of food and patch types (Mac Arthur and Pianka 1966, Royama 1970, Rapport 1971, Schoener 1971, Pulliam 1974, Charnov 1976, Estabrook and Dunham 1976, Pyke et al. 1977, Krebs 1978). This widespread interest is partly due to the potential range of application of foraging theory. Assumed relations between food availability and feeding behavior have already proved useful in studies of populations and communities of organisms (Mac Arthur 1972, Roughgarden 1974, Wilson 1976, Werner 1977).

Caution is required, however, when one attempts to apply simple models of foraging to complex communities (Schluter 1981). It is possible that many of the assumptions incorporated into the theory do not hold very far outside of it. We still know very little about predator choice in nature in relation to the efficiency with which foods may be exploited, and of changes in feeding behavior when environmental circumstances vary.

The diets of Darwin's ground finches have recently been the subject of detailed research (e.g., Abbott et al. 1977, Smith et al. 1978, Grant and Grant 1980). They moreover provide an example of an apparent

contradiction of optimal diet models: whereas theory predicts that animals should generalize their diets when food abundance declines, Smith et al. (1978) observed that ground finches specialized. However, the relationship between diet and food and patch profitability was not known, and changes in the quality and relative availability of foods between seasons was not accounted for. It was not determined whether the finches had significantly altered their preference for foods, or indeed patches, as the absolute and relative quantities available changed.

I thus undertook a field study to investigate more closely the diets of three species of Darwin's ground finches. Specifically, I attempted to answer these questions:

- 1) Do the finches select the most profitable foods and patches? Optimal foraging theory predicts that they should.
- 2) What is the relationship between seed choice and patch choice? Theorists have paid attention to aspects of diet and patch choice separately but few have considered how the two may interact.
- 3) Do ground finches generalize as food availability declines? They should, according to theory.

In this study I could not assume a priori the unit of resource as perceived by the finches. Instead, I considered aspects of diet in relation to both seed and patch types, in turn.

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This is not a test of the assumption of optimal feeding. Rather, the data are used to test whether the predictions of optimal foraging theory hold in a field situation.

METHODS

Study sites

The study was carried out on Isla Pinta (Abingdon) in the Galápagos archipelago between January and December 1979. Six study grids of 1 ha each were spaced ≈ 0.5 km apart along the southern slope, spanning in total the elevations 110–500 m above sea level. In connection with a second study, data on finch diets and food availability were collected from all sites. However, since the diversity of foods declined rapidly with increasing elevation, I used only the data recorded for the lowest two grids in the present analysis. The lower of these, grid 1 (at 110 m), was situated in the arid zone (Wiggins and Porter 1971) and was characterized by a smooth pahoehoe lava substrate, a moderate density of *Bursera graveolens* trees, scattered *Castela galapageia* shrubs, and numerous low-lying herbs and shrubs (notably *Alternanthera filifolia* and *Chamaesyce punctulata*). The second grid (180 m), best described as lower transition zone (Wiggins and Porter 1971), was distinguished by its abundance of *B. graveolens*, a relatively dense understory of *Scalesia incisa*, and a broken lava surface. *Rynchosia minima* and the grasses *Paspalum galapageia* and *Setaria setosa* were the predominant forms of ground cover.

Five species of ground finches (*Geospiza* Gould) coexist on Pinta: *G. fuliginosa*, *G. fortis*, *G. magnirostris*, *G. difficilis*, and *G. scandens*. The first three are the subjects of this study, though due to the greater diversity of seed types in its diet, most analysis is restricted to *G. fuliginosa*.

Climatic conditions in the Galápagos vary seasonally (Wiggins and Porter 1971, Grant and Boag 1980). Two seasons are recognized: the hot-wet and the cool-dry. The former typically extends from late December to May or June, the latter for the remaining months. Heavy and infrequent rainfall between December and May determines the duration of major seed and fruit production, and greatest activity of arthropods. The finches typically breed only in the wet season.

There is evidence that ground finch numbers are limited by the availability of seeds and fruits in the dry season (Smith et al. 1978). I therefore visited Pinta on four occasions for periods of 5–6 wk. These observation periods corresponded to the early and late wet season (20 January–28 February, 6 April–29 May) and the middle and late dry season (9 August–15 September, 28 October–3 December). Seed production was greatest during the first two visits, though some seed was produced at all visits.

Food availability

Methods of estimating seed density followed Abbott et al. (1977). Samples were collected during the middle

2 wk of each of the four observation periods. Quadrats of 1 m² were chosen using random numbers, and within these the number of seeds on the vegetation was determined. Also counted in quadrats were the seeds in the soil or on the rock surface in two corner subquadrats (0.125 m² each); these counts were multiplied by eight and added to the number of seeds on the vegetation to yield the quadrat total. Percent cover of plant species was estimated by eye. Twenty-five quadrats were sampled in grid 2 per visit. In grid 1 I sampled 25 times in February, and 50 times during each of the three subsequent visits. I doubled the sampling intensity in order to obtain density estimates for the greater diversity of seeds and plants in grid 1. Time restrictions prevented me from doing likewise in grid 2. All plants were identified with the aid of Wiggins and Porter (1971).

Air-dried samples of seeds of each species were collected in vials, and dimensions (Abbott et al. 1977) and dry masses of oven-dried seeds were determined in January 1980.

Diets

Methods of collecting data on finch diets differed slightly from those of Abbott et al. (1977) and Smith et al. (1978). Finch diets were quantified by systematically walking through the grid and recording the amount of time birds were observed to forage on each food type. Routes for these walks were selected so that I could scan the entire grid in an observation bout of a morning's or afternoon's duration; routes were altered on a daily basis. I set an upper limit of 300s/bird to allow observations on as many individuals as possible. Feeding walks were conducted from either 0630 to 1130 or 1500 to 1730. I spent 7 to 11 mornings or afternoons in each grid during each study period.

Finches removed seeds from both the ground and vegetation. Seed type could usually be identified in their beaks or, indirectly, by the parent plant. Seed handling times, defined as the total time required to crack and consume a seed from the moment it is held in the beak, were recorded with a stopwatch. From April to December rates of seed intake were also recorded, when possible. These rates refer to the number of seeds of each type that were seen to be consumed in the limited time interval that close visibility allowed. Intervals varied from 20 to 300s in duration. If a finch switched from feeding on a run of one food type to another during an observation period, the harvesting rates for different seed types were recorded separately. No more than two rate observations were recorded per finch encountered.

For several seed types handling of individual items was often impossible to observe, and rates were obtained indirectly. For *Alternanthera filifolia*, *Bouteloua disticha*, *Portulaca* sp. and, in August only, *Trichoneura lindleyana*, I recorded the number of whole seed heads manipulated in the beak during the obser-

TABLE 1. The proportion of feeding time devoted to seeds and fruits (= diet proportions) by ground finches. Total observation time in seconds and total number of birds are given in parentheses. Study periods A to D refer to the months January–February, April–May, August–September, and November–December, respectively.

Site	Study period	Diet proportion		
		<i>G. fuliginosa</i>	<i>G. fortis</i>	<i>G. magnirostris</i>
1	A	.47 (8 770/47)	.60 (2515/16)	.61 (1970/9)
1	B	.71 (15 170/78)	.76 (8100/39)	.96 (7820/30)
1	C	.92 (25 365/106)	.97 (7380/60)	1.00 (5320/25)
1	D	.77 (25 430/96)	.96 (7430/31)	1.00 (9400/37)
2	A	.79 (8 135/40)	.71 (2515/21)	.77 (3915/19)
2	B	.80 (8 875/53)	.78 (3585/17)	.96 (3320/16)
2	C	.91 (19 735/97)	1.00 (2865/14)	1.00 (320/2)
2	D	.78 (18 775/71)	1.00 (1930/9)	1.00 (180/2)

vation period. I later sampled 10 seed heads from the same location and counted the number of seeds in each. The number of seeds per head was highly uniform; the most extreme range of values was zero to five, for *A. filifolia*, and this was rarely realized in a given sample of 10. By multiplying the mean number of seeds per head (of the 10) by the number of heads manipulated by the finch I obtained an estimate of seed intake. This assumes that all seeds in a head are eaten; the remnants that I found of heads opened by finches support this assumption.

When a finch removed *Heliotropium angiospermum* from the ground the seeds were difficult to count in the beak, but distinct and audible snapping sounds were produced while the seed was crushed in the mandibles. I assumed that a single or rapid burst of snaps corresponded to a single half-fruit (or pair of seeds), the form in which they are most commonly encountered on the ground on Pinta.

Finch numbers

Finches were mist-netted on two successive days in each grid and study period. The basic procedure used was that of Abbott et al. (1977). Generally, two nets of 12-m length were unfurled at 0700 and these remained open for a total of 2.1h each day. There was one exception to this: in August–September netting began at 1500 to avoid the heavy morning mist (garúa) which descended regularly. Two nets were used in the first period (January–February), and three were used in each of the remaining three periods. The netting procedure gave similar results to those of another census method, transect counts, employed concurrently (D. Schluter, *personal observation*).

Analysis

In April–May only data from adult finches were used because juveniles were less efficient when feeding and tended to feed differently from adults (e.g., Grant and Grant 1980). Later in the year I could not distinguish adults from 1st-yr birds either by plumage, beak coloration, or general feeding efficiency and so I included data from all birds. Though finches ate a

variety of food types, most feeding effort was directed toward seeds, especially during the later periods (Table 1). I restricted the analysis to seeds and fruits because it proved difficult to obtain comparable estimates of the availabilities of other food types (e.g., nectar). I considered unripe and mature seeds and/or fruits of the same species to be different "seed types" as they possessed distinct dry masses and generated different handling times (e.g., *Rynchosia minima* and *Heliotropium angiospermum*).

Rate of seed intake was analyzed using the regression model $Y = bX + e$ (Snedecor and Cochran 1967), where Y is the number of seeds harvested in a feeding period of duration X seconds. Since the intercept is zero, b is the weighted mean rate of seed intake for that seed type and is estimated by $\Sigma Y/\Sigma X$. The deviate, e , is assumed to be normally distributed with mean zero and variance proportional to the magnitude of X . Standard errors and 95% confidence intervals for b were computed (Snedecor and Cochran 1967). These values were multiplied by the mean dry masses of the seed types to yield means and confidence limits for the rates of dry mass intake.

I have calculated from the data given in Willson (1971; Table 1) that mean whole seed biomass of individual seed types was correlated with mean total energy of seed kernels ($N = 8$, $r = .999$, $P < .01$). Here I assume that dry mass of whole seeds and energy content are equivalent.

In order to estimate seed intake rates for some items that were infrequently consumed I was forced to substitute rates obtained in another grid, or to average rates taken over several adjacent grids. This was done only when rates on a given seed type were consistent among grids. In addition I assumed the feeding rate of *G. fuliginosa* on the tiny seeds of *Eragrostis ciliaris* to be the maximal rate of seed intake. This latter rate was measured as the rate at which tiny tea-biscuit crumbs were ingested when offered on a flat board surface.

Definitions

A patch is here loosely defined as a cluster of seeds of the same type. Such clusters were prevalent in the

TABLE 2. Mean handling efficiency of finches on several seed types in grid 1. Handling efficiency is defined as seed mass divided by the mean handling time for that seed. Seed depth of *Rynchosia minima* (green fruit) is unknown, so that of the mature seed is listed instead. Underlining indicates that differences in mean handling time are not significantly different ($P > .01$, Student's t tests). A dash indicates that efficiency was not measured but is assumed to be negligible (see text).

Seed type	Mean seed depth (mm)	Handling efficiency (mg/s)		
		<i>G. fuliginosa</i>	<i>G. fortis</i>	<i>G. magnirostris</i>
<i>Aristida repens</i>	0.33	0.05	?	?
<i>Cyperus andersonii</i>	0.57	0.09	?	?
<i>Setaria setosa</i>	0.74	0.18	0.16	?
<i>Paspalum galapageia</i>	0.98	0.27	0.24	0.23
<i>Scalesia incisa</i>	1.24	0.16	?	?
<i>Cenchrus platyacanthus</i>	2.11	...	0.66	0.72
<i>Lantana peduncularis</i>	2.15	...	0.29	0.26
<i>Rynchosia minima</i> *	(2.45)	0.88	1.76	1.82
<i>Bursera graveolens</i>	4.16	...	0.49	1.51
<i>Opuntia galapageia</i>	4.58	0.96
<i>Castela galapageia</i>	6.59	4.03
Mean beak depth of finch species (mm)†		7.7	11.8	20.0

* Green fruit.

† Males only; data from Lack (1947).

study grids, especially since seeds were characteristically associated with the individual plants that had produced them. Partly as a result, finches frequently consumed seeds in runs, uninterrupted sequences of items of the same type. However, I was unable to conceive of a measure of environmental "patchiness" that would reliably reflect the perception of food distribution by finches. Instead I recognized a patch by the restriction of a bird's foraging to a single seed type, and a patch type as the plant species yielding the specified seed type.

Foraging efficiency refers to the rate at which finches obtain food (biomass), whether on single seeds or patches. Handling efficiency is the foraging efficiency on individual seeds, measured as the mean dry mass of a given seed divided by its mean handling time. Profitability is the mean foraging efficiency within patches of a given type, and is the slope, b , of the regression model (see Methods). Both profitability and handling efficiency may refer to foraging efficiency on the same seed type. However, profitability includes the search time between individual seeds whereas handling efficiency ignores this element.

RESULTS

Diet and foraging efficiency

Optimal foraging theory predicts that food and patches with highest energy rewards should be selected by predators. I tested this prediction for seed and patch types by comparing foraging efficiency with diet for three species of ground finches.

The efficiencies with which seeds of various sizes (depths) are handled by finches are listed in Table 2. Seed depth is the intermediate of the three orthogonal

dimensions, length, depth, and width, and is correlated with dry mass ($r = .92$, $N = 22$, $P < .01$). Beak depths of finch species (Lack 1947) are also presented for comparison (Table 2); other morphological traits which distinguish the species covary with beak depth (Abbott et al. 1977). Where dashes are shown (Table 2), no handling times were obtained, but negligible efficiencies are assumed. It is probable that these larger seeds are beyond the cracking capacity of the smaller finches. Individuals of *G. fortis*, the medium-sized finch species (Table 2), have not been seen to attempt to crack any seed larger than that of *Bursera graveolens*. These seeds themselves are difficult for *G. fortis* to deal with (compare with *G. magnirostris*, the largest finch species), and many are discarded without being opened. Of 31 observations of *G. fortis* individuals attempting to crack *B. graveolens* seeds, 7 were unsuccessful and the seeds were abandoned after 5–120 s.

Similarly, excepting the soft green fruit of *Rynchosia minima*, *G. fuliginosa* individuals are probably unable to break open seeds as large as *Lantana peduncularis*. I only once observed this finch species attempting to crack a mature *L. peduncularis* seed, but the seed was abandoned after 20 s. The upper limit in the size of a seed allowing successful cracking is therefore related to finch beak size, and is larger for larger finches (see also Grant et al. 1976, Abbott et al. 1977). In addition, handling efficiencies for all three species are similar on the small seeds, *Paspalum galapageia* and *Setaria setosa*, and for *G. fuliginosa* and *G. fortis* it is not until the upper size limit is approached that efficiency drops below that of the adjacent larger finch species (Table 2). Also, for each species, handling efficiency tends to be greater on the

TABLE 3. Comparison of *G. fuliginosa* preference with seed depth (I), and diet proportions with patch type profitability (II). Comparison I uses Spearman rank correlations, and II uses partial correlations between the two variables holding the effect of plant frequency of occurrence fixed (log transformations of all three variables). Asterisks indicate one-tailed levels of significance. Study period symbols as in Table 1. The same seed types were used in both comparisons.

Grid	Study period	N	Correlation coefficients	
			Comparison I	Comparison II
1	B	15	.44*	.55**
1	C	11	.88**	.67**
1	D	9	.58*	.78**
2	B	10	.34	-.04
2	C	11	.60**	.11
2	D	11	.44	.34

* $P < .10$; ** $P < .05$.

larger seeds that it is able to utilize, though the pattern is irregular. A similar trend is indicated by patches (Fig. 1B). The mean profitability of the patch types used by *G. fuliginosa* tends to increase with the size of the constituent seed type. The larger finch species exploit the larger seeds with even greater efficiency (Fig. 1B).

Thus from considerations of foraging efficiency we may expect that the range of seed depths used by different finch species should reflect the position of their upper handling limit. This seems to be the case (Fig. 1A). In August–September in grid 1, *G. fuliginosa* concentrated on the small seeds of *Chamaesyce punctulata*, and took items as large as the green fruit of *R. minima*. *G. fortis* collected mainly the medium-sized mature seeds of *Cenchrus platyacanthus* and *R. minima*. *G. magnirostris* specialized on seeds of *Opuntia galapageia*. The two larger finch species spent little time feeding on small seeds, and the two smaller species allocated no time toward seeds apparently too large and hard to crack. The pattern was highly similar in the other study periods and grid, and agrees with expectation.

Diet, foraging efficiency and relative food availability

Table 2 and Fig. 1 suggest that diet and foraging efficiency are related, but diet proportions are not well predicted by this measure. For example, in *G. fuliginosa* diet proportions are quite low for larger seed types though foraging efficiency is maximal on these. An obvious explanation is that availability of foods also influences diet. In this section I compare diet with both food availability and foraging efficiency. A positive association is expected between an item's representation in the diet and the efficiency with which it is harvested, when the relative abundance of items

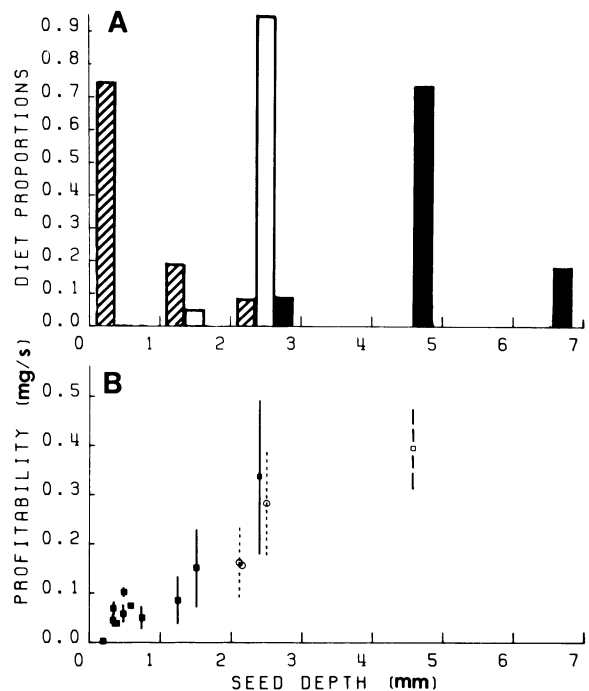


FIG. 1. (A) The proportion of feeding time spent feeding on seeds of various depths (= diet proportions) by three ground finch species in August–September (period C) in grid 1. Finch species are *Geospiza fuliginosa* (hatched bars), *G. fortis* (open bars) and *G. magnirostris* (solid bars). (B) The profitabilities of patch types containing seeds of various depths in the same period and grid. Vertical bars delimit the 95% confidence intervals for the means. Where no intervals are provided, data points are indirect estimates (see Methods). Finch species are *G. fuliginosa* (—■—), *G. fortis* (—○—) and *G. magnirostris* (—□—).

is taken into account. This detailed analysis is restricted to *G. fuliginosa*.

Seeds.—I computed seed preference values using Jacobs' (1974) index, $\log Q$. This measure is an adjusted ratio of the proportion of a given seed type in the diet to that in the environment. Where, through inadequacies in sampling, the proportion of available seeds of a given type was recorded as zero yet the proportion of this food in the finches' diet was positive, an arbitrary small number equal to one-half the smallest nonzero value was substituted. Deleting these rare foods does not greatly alter the results. Zero values for diet proportions were treated similarly so that logs could be taken. Rank correlations (see later) are unaffected by this step.

Ideally, seed preference should be compared with handling efficiency; unfortunately such data exist for only a few seed types, too few for analysis. Data in Table 2 suggest that for *G. fuliginosa* handling efficiency, where not zero, is positively correlated with depth of the seed type ($r = .91$, $N = 6$, $P < .01$). Assuming this to be true in general, Spearman rank correlation coefficients (Snedecor and Cochran 1967)

TABLE 4. Stepwise linear contribution of the two independent variables, profitability (X_1) and frequency of occurrence (X_2) to the total variance in the dependent variable, diet proportions. Data are a pooled sample of all study periods in grids 1 and 2 (*G. fuliginosa* only). Model uses log transformations of all three variables. $N = 67$.

Step	Variable	R^2	Significance of regression	Significance of coefficient	Regression model
1	Profitability	.311	<.001	<.001	$Y = .802X_1 - .376$
2	Frequency	.398	<.001	.004	$Y = .604X_1 + .566X_2 - .398$

were computed comparing preference with depth (Table 3). To be consistent with the second part of this analysis, the comparison was restricted to the same seed types and study periods for which profitability data exist. All six coefficients are positive (Table 3), and four are significant at the .10 or .05 level. Finches tended to prefer the larger seeds that they were able to utilize, and these provided them with the greatest biomass per unit handling time.

Patches.—As a measure of patch abundance I used the number of 1-m² random quadrats in which a given plant species was found, scaled to a percentage (hereafter called frequency of occurrence). I later repeated portions of the analysis with percent cover instead: results were very similar. Neither of these two measures of patch abundance is correlated with the numerical abundance of the corresponding seed type ($P > .05$). To test the prediction that diet is related to the rate of intake within patches I compared patch type profitability with the ratio of seed proportions in the diet to plant frequency of occurrence. Only one of six such associations is significant ($P < .05$).

Patch type profitability is highly correlated with plant frequency of occurrence (five of six comparisons significant, $r = .64-.93$, $P < .05$) a relation which might obscure any association between patch preference and profitability. Moreover, it is probable that this correlation is accidental, since profitability is here defined as mean biomass intake for runs of a particular seed type, a measurement restricted to a plant or plant cluster. The most valuable patch types merely happened to be the most common ones; the difficulty is to separate the effects of these variables on the choice of diet items.

To this end I computed partial correlations between diet and profitability while fixing the effects of frequency of occurrence (Snedecor and Cochran 1967). Log transformations of data were used to correct for heteroscedasticity. Also, the log-log model is appropriate since it tends to compare diet with profitability relative to patch abundance.

Partial correlation coefficients are listed in Table 3. Of six correlations, three are significant: those in grid 1. It is noteworthy that the highest linear correlations between plant frequency of occurrence and profitability of patch types were obtained in the second grid. Thus the small partial coefficients here do not necessarily indicate that that diet is unrelated to feeding

efficiency in patches. They merely show that the effect of profitability could not be separated from that of patch abundance. This is because little residual variance remained after the effect of frequency of occurrence was removed. In grid 1 profitability-patch abundance correlations are uniformly weaker than in grid 2. As Table 3 indicates, the results in this grid are in agreement with expectation.

This analysis was extended to investigate the individual and combined abilities of patch profitability and frequency of occurrence to predict diet. I performed a two-step multiple linear regression (Snedecor and Cochran 1967) on the pooled data from all grids and periods. As ranges of values obtained for these variables differed among samples, the data were adjusted onto a common scale by dividing the values for each variable by the sample standard deviation. Variables used were log transformations of these data. Frequency of occurrence and profitability were considered the independent variables, and their stepwise contribution to the variance in diet proportion is shown in Table 4.

The first variable selected by the procedure was patch profitability, with plant frequency of occurrence explaining some of the residual variance. Together the two account for nearly 40% of the total variance in diet proportions.

These results do not illuminate the causal relationships among the variables nor do they rule out the possibility that alternative variables (or indeed statistical models) may better "explain" patch selection by *G. fuliginosa*. However, the data do indicate that patch type profitability and diet are significantly correlated when the effects of patch abundance are held constant. This relation is consistent with the prediction of optimal foraging theory.

In summary, *G. fuliginosa* preference for seed types was correlated with seed depth within the range of sizes consumed. Proportions of foods in the diet within this same range are correlated with patch type profitability when the effects of patch frequency of occurrence are fixed. The results agree with expectation.

Seasonal changes in diet breadth

Ideally the theory of optimal diets should be employed to predict exactly the diets of organisms under varying circumstances. In a complex environment the amount of data required would probably be prohibitive. However, a useful prediction of the theory is that

TABLE 5. Food density, mean feeding rate, and density of *G. fuliginosa*. SE's of mean total food density are provided as a measure of scatter only; means are not derived from normally distributed data. Bird density is the total number of *G. fuliginosa* netted in the census (data from period A are adjusted to three nets). See text for explanations of other headings. Within grids, study periods are ranked on the basis of food availability. Period symbols as in Table 1. Feeding rate was not measured during January–February.

Grid	Study period	Season	Total food density* \pm SE (mg/m ²)	Rank	Bird density (three nets)	Food density per bird	Mean feeding rate (mg/s)
1	A	Wet	426.6 \pm 138.7	2	13.5	31.6	. . .
1	B	Wet	542.8 \pm 86.4	1	47.0	11.6	.200
1	C	Dry	27.1 \pm 5.2	3	12.0	2.3	.069
1	D	Dry	23.9 \pm 7.5	4	30.0	0.8	.047
2	A	Wet	254.8 \pm 68.2	2	9.0	28.3	. . .
2	B	Wet	659.0 \pm 143.9	1	55.0	12.0	.182
2	C	Dry	66.5 \pm 14.7	3	16.0	4.2	.167
2	D	Dry	35.1 \pm 5.5	4	19.0	1.9	.155

* *Rynchosia minima* (mature seed) and *Cenchrus platyacanthus* excluded.

organisms should generalize their diets as food becomes scarce (Mac Arthur and Pianka 1966, Schoener 1971). I here examine diet breadth of *G. fuliginosa* and compare it among seasons, and hence different food availability conditions. First, preference measures are computed which estimate the ratio of relative use of individual seed types to their relative availability. This procedure permits direct contrasting of selectivity of specific seed types. Second, I compare diet breadth when seed types are grouped into five seed-depth categories. The ability of handling efficiency and patch type profitability to explain diet selectivity and content statistically is also contrasted among study periods.

Food abundance and finch density.—Two measures of food abundance are compared among seasons in Table 5. Food density is the mean density of sampled seeds which are known to be eaten by *G. fuliginosa*. Two seed types, *Rynchosia minima* (mature seed) and *Cenchrus platyacanthus*, were excluded as they are large, abundant, and eaten very infrequently. Mean feeding rate is the sum of the mean profitabilities of patch types multiplied by the proportion that the corresponding seed type contributes to the diet. Rates are available for three of four study periods. Seed types for which no estimate of profitability could be made are not included in this measure; however, since patch profitabilities were obtained for all foods commonly eaten, the sum is little influenced by their absence.

Total food density varied significantly among study periods in both grids (Kruskal-Wallis test [Gibbons 1971], $P < .001$). Food density was maximum in period B, and its major decline occurred between between periods B and C (Table 5). In grid 1, mean feeding rate decreased sharply over the same interval, while in grid 2 feeding rate declined less, and rather evenly over periods B to D. Seasonal variation in this mean cannot be compared statistically, but the distribution of single observations of feeding rate (see later and Fig. 4) varied significantly in grid 1 (Kruskal-Wallis test, $P < .001$). This was not the case in grid 2 ($P = .23$).

Food types available to and consumed by finches did not differ greatly among seasons within a site. Important exceptions were *Portulaca* sp., *Setaria setosa*, *Paspalum galapageia* and *Boerhaavia caribaea* in grid 1. These plants were almost absent from this grid in all periods but the second (April–May). The green fruit of *Rynchosia minima* was essentially absent from the same grid only in period D. When available, all these seed types were components of *G. fuliginosa*'s diet. Thus in grid 1 only, the diversity of available foods declined somewhat with decreasing food abundance.

Finch density increased dramatically between the first and second periods (Table 5). As breeding had commenced by late January and was nearly over by May, the difference in density can be attributed to recruitment of juveniles into the population. Densities declined irregularly thereafter. Despite a decline in food abundance between periods C and D, the number of finches netted actually increased. I suspect that this is due to the greater mobility of finches in the late dry season. Smith et al. (1978) discuss in more detail the problems inherent in the mist-netting technique.

Food density per bird is the ratio of total seed biomass per unit area to the number of finches netted (Table 5). Values are highest at the onset of breeding (period A) and decline steadily into the dry season. If

TABLE 6. Comparison of food preference by *G. fuliginosa* between adjacent study periods. VAR is the variance of log Q . Symbols as in Table 1.

Comparison (1 vs. 2)	Grid	N	VAR 1/VAR 2	
			Predicted	Observed
A vs. B	1	10	<1	1.09
B vs. C	1	13	>1	0.60
C vs. D	1	11	>1	1.77
A vs. B	2	7	<1	2.28
B vs. C	2	10	>1	0.83
C vs. D	2	10	>1	0.23

bird density, as measured by mist-netting, is artificially high in period D, then values for food density per bird here might be underestimates. Nevertheless it is apparent that both total food abundance and the quantity of food available per bird declined from period B to D.

Roughly equivalent seed densities in both grids did not result in comparable feeding rates. This is partly a consequence of the different patch types available in each. For this reason grids are analyzed separately. For simplicity, each period was assigned a rank position determined by the quantity of food available (Table 5).

Seeds.—If *G. fuliginosa* generalized as food became scarce we would predict that its diet should more closely have reflected availability in the dry season than in the wet season. This was tested by contrasting preference between adjacent study periods in each grid (Table 6). Seed types that were "absent" (i.e., no seeds found in the random samples) from either of the two periods under consideration were of necessity excluded, as were seed types not eaten by *G. fuliginosa* in both periods. For the resulting subset of seed types, I recomputed diet and available proportions. This procedure was repeated for each adjacent pair of study periods. As before, zero values for proportions in the diet were replaced with an arbitrary low figure so that logs could be obtained.

Selectivity, or preference, was determined using Jacobs' (1974) index, $\log Q$. The log transformation provides a symmetrical scale about zero (Cock 1978) and preference of a food may be directly compared among seasons. A $\log Q$ value of zero indicates no preference by finches, and a nonzero value indicates positive or negative selection for the seed type. For example, diet preference for *R. minima* (green fruit) was 1.95 in period A and 1.45 in B (A vs. B comparison). Selectivity for this food thus declined. If finches' choice of foods more closely matched available densities one would expect the variance in preference values to diminish. The ratio of variances in preference between study periods thus provides an index of change in diet breadth. These values are compared with predicted trends in Table 6. Of six comparisons only one is in the expected direction. Since preference values for seed types within a study period are not independent measures I cannot assign probabilities to the results. Nevertheless there is no indication that finches became less selective in their choice of foods as food levels dropped.

Optimal diet theory predicts that foods of lower value should be sequentially added to the diet as food availability declines. Thus the range of items exploited should increase. However, in this study there was no seed type which, if present in any two periods, was eaten in only one of the periods. Consequently the number of items in the diet did not increase when food became more scarce.

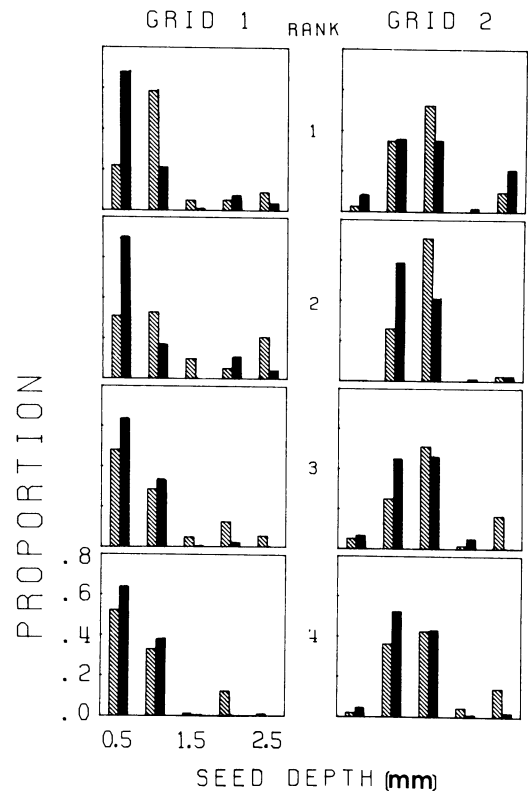


FIG. 2. Observed contributions of seeds of various depths to the diet of *Geospiza fuliginosa* (hatched bars) compared with available proportions (solid bars). Study periods are ranked in each grid from highest to lowest food availability (see Table 5).

Models of optimal diet generally rank foods on some functional basis, usually handling efficiency (e.g., MacArthur and Pianka 1966). If this attribute is important in determining seed choice then we would expect the diversity of categories of seeds based upon handling efficiency to increase as food levels decline. It was observed earlier that seed depth and handling efficiency are correlated for *G. fuliginosa* (Table 2). Seed types were therefore grouped into five seed depth classes (0.0–2.5 mm by 0.5-mm increments). With the exception of those foods whose exclusion is mentioned in Table 5, all seed types eaten at least once during the year were included. Diet and available proportions of seed types within these categories are diagrammed in Fig. 2.

To compare diet breadth of *G. fuliginosa* among seasons on these categories I used S , actually the Renkonen-Whittaker similarity or "niche overlap" (Hurlbert 1978) between the distribution of food selected and that available (Fig. 3). In grid 2 no consistent trend for this index is observed. In grid 1, however, some tendency toward diet generalization is indicated.

The index, S , is a function of the absolute difference between use and availability. As can be seen by in-

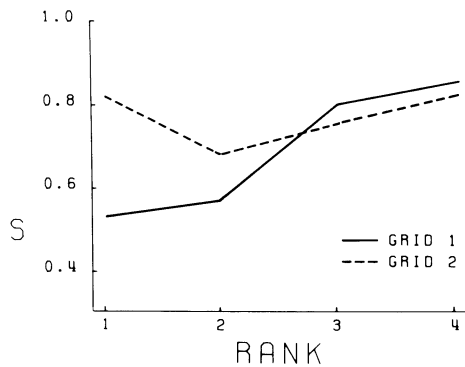


FIG. 3. Diet diversity in relation to food abundance. Data used are the proportions of seeds available (q_i) and in the diet (p_i) that are of seed depth i . Proportions are as illustrated in Fig. 2. Food abundance ranked from high (1) to low (4) as in Table 5. $S = 1 - (1/2)(\sum |p_i - q_i|)$ (Hurlbert 1978). A result of 1.0 indicates the most general diet, and 0.0 indicates the most specialized diet.

specting the data shown in Fig. 2, part of the increase in S may be attributed to an expected bias: certain categories of seeds become rare as food levels decline, and the proportions of these seed types in the diet (and hence the difference between diet and available proportions) diminish as a trivial consequence. The value of S is thus inflated, even though selection for rare sizes of seeds may be constant. There is one notable change nonetheless: in all seasons, seeds of the shallowest depth category are most abundant. Their representation in the diet is, however, comparatively small until periods C and D when they become predominant. The observed increase in S in grid 1 may be attributed to this shift. This outcome agrees with expectation: if depth is a reliable index of handling efficiency then in grid 1 *G. fuliginosa* altered its diet toward feeding on seeds of lower value.

It is worth stressing however that this analysis assumes that the birds were choosing seeds on the basis of handling efficiency and that search time between seeds was of secondary importance. What might be expected if instead the finches selected foods on the basis of expected profitability of patch types? In grid 1 during study period B patch types of common seeds of depth class 0.5–1 mm were considerably more profitable than those of the smallest depth class (see Appendix: compare *P. galapageia* and *Portulaca* sp. with *Chamaesyce punctulata* and *Aristida repens*). In both periods C and D these same depth class 0.5–1 mm seeds were rare or absent altogether, and the most valuable seed type within these two classes is a member of the 0–0.5 mm class: *C. punctulata*. No comparable change occurred in the second grid. Thus the apparent diet generalization exhibited by finches in grid 1 may be a mere consequence of selection for profitable patch types.

Patches.—If patches rather than seed types deter-

mine the optimal diet we would expect that finches become less selective in their choice of these as food availability declines. Table 5 demonstrates that, while overall food quantities declined dramatically (16- to 23-fold), feeding rate within patches decreased to a smaller degree (1.5- to 4.2-fold). The implication here is that a reduction in the size and quantity of patches in the dry season was the main "cause" of the reduction in food abundance. In such circumstances a predator should not overlook patches of poor quality (MacArthur and Pianka 1966).

Since patch types did decline in profitability nonetheless (see Appendix and Table 5), the comparison of diversity of patch types exploited is not an appropriate test for decreased selectivity in the choice of these. I have attempted to detect generalization of patch use in two ways. First, the utilization of patches of various rewards is compared among seasons; second, the relative ability of patch type profitability and abundance to explain diet statistically is contrasted among seasons.

Foraging theory predicts that at high resource densities finches should ignore patches of low profitability. As food abundance decreases, patches of lower value should be added to the foraging itinerary. The range and distribution of single observations of feeding rate irrespective of duration or type are illustrated for grid 1 in Fig. 4. If we assume that each rate observation of *G. fuliginosa* shown corresponds to an environmental patch with profitability approximately equal to the harvest rate recorded, then Fig. 4 essentially describes the patch itineraries at different periods. Note that as food abundance declined, the range of harvest rates recorded also decreased ($P < .001$, see earlier). This corresponds to a smaller modal efficiency exploited in the later periods. Note also that observations of low harvest rewards were recorded in all seasons, but finches were more likely to feed in patches of low profitability in period D than during any other. Unfortunately one would require a knowledge of the quantity of patches of various profitability in each season before it could be known whether finches had actually altered their preference. The distribution of mean profitabilities of patch types available (Fig. 4) suggests that changes in the range and variance of harvest rates recorded might reflect underlying changes in availability rather than an altered foraging tactic by *G. fuliginosa*. This aspect is tested for individual patch types shortly. Nonetheless, the prediction that finches feed in poor patches only when food is scarce is contradicted by these data. Possibly this is a result of sampling or information gathering by the birds (cf. Royama 1970, Krebs et al. 1978).

If fewer patch types of inferior quality are overlooked when food is scarce, then patch type profitability should diminish in importance as a determinant of diet, relative to that of patch type abundance. Earlier, a two-step linear regression demonstrated that

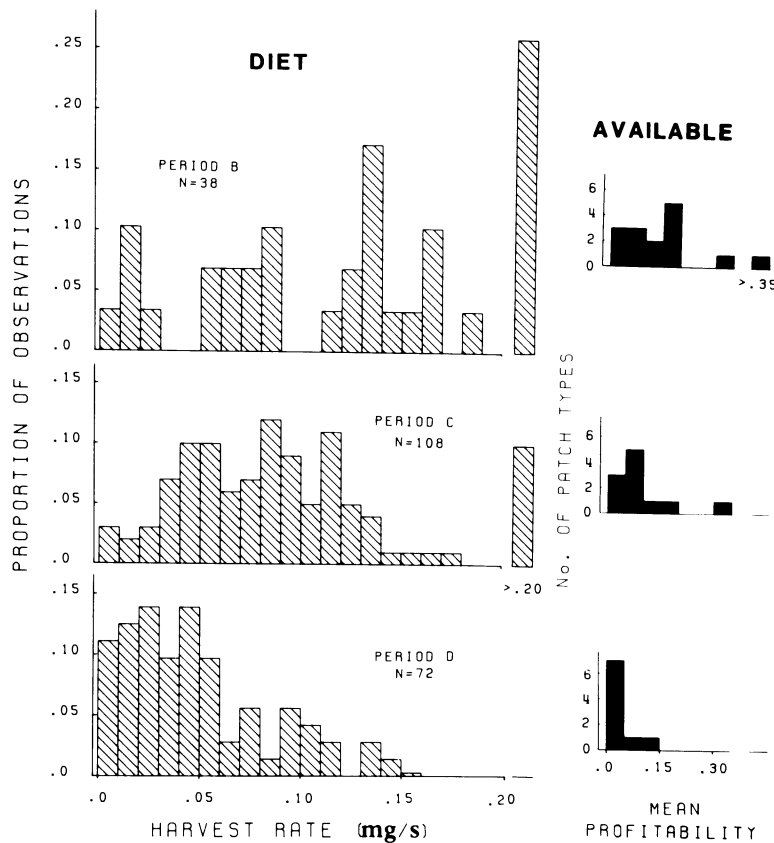


FIG. 4. Frequency distribution of feeding rate observations converted to milligrams per second for *Geospiza fuliginosa* in grid 1. For comparison, the frequency distribution of mean profitability of patch types available is shown to the right of diet values.

both profitability and frequency of occurrence were significant in explaining the total variance in the proportions of foods in the diet. To test whether the importance of these variables changed seasonally as predicted, I constructed best-fit multiple regressions of diet proportions on both for each grid and period. Again log transformations of data were used. The relative importance of the independent variables was investigated by comparing the standard partial regression coefficients (Snedecor and Cochran 1967). These values refer to the increase in the magnitude of the dependent variable, diet proportions, per unit increase in either independent variable, in units of standard deviations. The independent variable with the larger coefficient is assumed to be the more important. The one-tailed significance of each coefficient was also computed. This measure provides a test of the null hypothesis that the coefficient is less than or equal to zero. Results are listed in Table 7.

Standard partial regression coefficients of diet on profitability are uniformly greater than those of frequency on diet in grid 1 and uniformly smaller in grid 2. The size of the coefficient on frequency shows a slight increase toward period D in grid 1, though the

relative importance of this variable is offset by a similar increase of the coefficient on profitability. In grid 2 the coefficient on profitability also increases yet that on frequency declines, the opposite trend to that found in grid 1. Few of the coefficients in grid two are significant, though the probability that the coefficient of diet on profitability is zero or less declines in the latter periods. The same trend in significance values is shown in grid 1.

It thus appears that the only pattern in the regression analysis consistent between grids is an increase in the standard coefficients for the partial regression of diet on patch type profitability and a corresponding decline in the probability that these coefficients are zero or less. Therefore, as food abundance declined the importance of profitability as a determinant of *G. fuliginosa*'s diet increased rather than decreased. The importance of plant abundance seemed not to change in a predictable fashion. Consequently there is evidence from these analyses that the finches did not generalize in their use of patch types. This result is inconsistent with expectation.

In summary, finches did not appear to generalize their diets as food levels declined. In grid 1 generali-

TABLE 7. Results of multiple linear regression of dependent variable, diet proportion, on patch type profitability (P) and plant frequency of occurrence (F). Data used are log transforms of original variables. All regressions are significant (one-tailed probabilities, $P < .05$). Study period symbols as in Table 1. Food availability ranks as in Table 5.

Grid	Study period	Rank	R^2	N	Standard partial regression coefficient		Significance of coefficient	
					P	F	P	F
1	B	1	.416	15	.509	.316	.021	.092
1	C	3	.681	11	.618	.300	.017	.125
1	D	4	.713	9	.659	.485	.012	.034
2	B	1	.526	10	-.045	.762	.537	.075
2	C	3	.594	10	.094	.707	.374	.022
2	D	4	.449	11	.300	.474	.171	.075

zation in the use of seed types of different depth was observed, but the result could be accounted for by considering that patch types of highest profitability were chosen by finches. Finches did not become less selective in their use of patch types. These data are not consistent with predictions from optimal foraging theory.

DISCUSSION

Did finches select the most profitable foods and patches?

In this study the size of individual ground finch species determined the overall range of seed depths chosen. For all three species the handling efficiency on seeds and the profitability of patch types were greater for large seeds, up to a point. This upper bound was greatest for *G. magnirostris*, the largest of the three species, and smallest for *G. fuliginosa*, the smallest species. Correspondingly, *G. magnirostris* and *G. fortis*, the medium finch, rarely consumed small seeds of low reward rate, and *G. fortis* and *G. fuliginosa* avoided seeds too large and hard to consume.

In addition, the diet of *G. fuliginosa* was determined by both the abundance of resources and the efficiency with which these could be exploited. Seed preference was correlated with the depth of the seed type, which is an index of handling efficiency, within the range of sizes consumed by *G. fuliginosa*. Seed proportion in the diet was correlated with the profitability of the corresponding patch type.

The data agree with expectation. Moreover, the results corroborate those of Davies (1977) and Goss-Custard (1977). These two studies showed that preference of wild birds could be attributed to differences in feeding efficiency on varying sizes of a single prey type. The present study has shown that similar preferences exist when prey types are taxonomically distinct (see also Zach and Falls 1978 and Pulliam 1980; but see Willson 1971).

Since the value of seed and patch types was computed from the dry masses of seeds, the implication is that finches selected seeds and patches mainly on

the basis of energetic rewards. However, it is worth recalling that only the seed portion of the diet was analyzed in detail. *G. fuliginosa* consumed arthropods in all seasons and probably obtained important nutrients from this and other food sources. In addition, preference was computed only for seed types eaten at least once in the year, of all those available, and feeding efficiency was estimated only for those commonly eaten.

Certain seeds which could provide significant energetic returns were thus excluded. For example, *G. fuliginosa* was never seen to consume seeds of *Borreria ericaefolia*, and it only rarely ate fruits of *Sida* sp., despite their abundance. Seeds of both species fall within the size range of seeds more commonly selected and this is reason to believe the finches may be quite efficient on these. Probably other components of foods (e.g., palatability, toxins, and nutrient content) influence choice (McKey 1979, Rapport 1980). However, by comparing diet to foraging efficiency on a restricted set of seed types I was able to minimize the importance of these factors.

In conclusion, ground finches did select foods on which handling efficiency was greatest and which occurred in patches of highest profitability. While not verifying the assumption of optimal feeding, the result is consistent with one of its expectations.

What was the relationship between seed choice and patch choice?

In any field study that attempts to determine whether resources are used efficiently, it is essential that the resources be correctly identified. I have avoided using a single description of resources, and instead partitioned the food spectrum into "seed types" and "patch types" in turn. Two ways in which the finches possibly perceived the environment were thus considered, and conclusions based upon one resource description may be compared with those of the second.

Smith et al. (1978) observed that the diets of ground finches were more specialized in the dry season, against expectation. The authors explained that their results were possibly a consequence of changes in the use of patches, an aspect that was not investigated.

The present study has carefully considered seed selection in relation to resource abundance and has shown that in only one of two grids studied did *G. fuliginosa* appear to alter its preference for seed types (Fig. 3). In doing so the species apparently generalized rather than specialized. Again, the diet shift could be interpreted as the outcome of selection by finches for profitable patch types rather than seed types. However, birds did not generalize their use of patch types. Evidently the results one obtains may depend upon the description of resources used. If there is uncertainty about the way in which a test organism partitions the food spectrum, then perhaps several possible descriptions should be considered.

Certainly the optimal diet will depend upon the way in which the food spectrum is utilized (e.g., McNair 1979, Heller 1980). If on Isla Pinta ground finches chose a diet on the basis of the handling efficiencies of seeds then profitable patches might have been overlooked. Conversely, if instead finches selected patch types by their profitability, then valuable seed types may have been avoided. In this case the extent to which a diet based upon patch characteristics could be predicted from the attributes of individual seed types would depend upon the strength of the relationship between patch profitability and seed handling efficiency. On Pinta the profitability of patch types and the handling efficiency on seed types for *G. fuliginosa* were both apparently correlated with seed depth (Table 2 and Fig. 1). However, since seeds tended to be eaten in runs of the same type, in at least several cases small seeds yielded higher returns when search time was accounted for than did larger seeds (see Appendix). A specific example is *Chamaesyce punctulata* (depth = 0.48 mm): in periods C and D patches of this seed type were more profitable than most larger seeds consumed at the same time.

These data suggest that diet choice based upon attributes of patch types would frequently have been more appropriate than an alternate strategy based upon seed types. Moreover, should *G. fuliginosa* have actually perceived the environment as consisting of patch types, then its use of individual seed types might have been a simple consequence of patch selection.

The difficulty of describing patches may be a limiting factor in the future study of patch choice. More important, however, than the description of "patchiness" in nature is the actual perception of patches by organisms (Wiens 1976). Patch types in this study were defined as runs of seeds of the same kind. Though these runs did correspond in some unmeasured way to clumps of seeds in the environment, the definition was a behavioral one: patches were recognized by discontinuities in the foraging behavior of the birds. In general, therefore, they need not reflect a spatial distribution of items at all. Food types requiring different foraging techniques in the same environment (e.g., Root 1967, Davies and Green 1976) are essentially in

distinct patch types. Search images may influence diets in exactly the same manner.

Field observations documenting changes in diet preference are becoming more frequent and often the data conflict with expectations from optimal foraging theory (Smith et al. 1978, Schluter 1981). The present study indicates that the ability to observe changes in predator specificity depends upon the observer's classification of "resources." If environments are patchy and food and patch characteristics do not coincide, then the abundance of items and the efficiency with which they are utilized will be inaccurate indices of feeding preference.

Did ground finches generalize as food availability declined?

Food availability and finch numbers declined dramatically between the beginning and latter part of the dry season. Total seed biomass fell at least sixteenfold and within-patch feeding rate decreased also.

G. fuliginosa did not select seed types in the proportions in which they occurred in the habitat. However, overall preference by this finch species for individual seed types did not change detectably when food availability declined seasonally. Use of seed types grouped into depth categories did change somewhat with season: in grid 1 *G. fuliginosa* allocated a relatively greater amount of time toward small seeds as the abundance of all sizes decreased. Thus diet breadth increased, but the result was not duplicated in grid 2. However, this change in the utilization of seeds in grid 1 could be explained by the observation that in the dry season, patch types of small seeds were more profitable than those of larger seeds, but only in grid 1. Finches did not generalize their use of patch types.

The results are thus partly ambiguous, and are not likely to be clarified simply. The major confounding aspect is the perennial question of resources: seeds or patches? Two lines of reasoning support the view that attributes of patch types predominated in determining finch diets on Pinta. First, the variables that best predict diet proportions in both study grids were patch type profitability and plant frequency of occurrence. When I repeated the analysis of Table 4, but included attributes of seed types in the regression (depth, numbers, and biomass), the results were unchanged. The additional variables did not contribute significantly to the total variance in diet proportion.

Secondly, as noted earlier, birds should not ignore small seeds of low individual returns if often they are very profitable by virtue of their high density within patches (e.g., *Chamaesyce punctulata*). It could be argued that theory is supported by the observed diet generalization (Fig. 3) but an additional explanation would be needed to account for why this was restricted to the first study site, and why seed types and not

patch types were the basis of food selection when the latter was probably more appropriate.

I therefore tentatively conclude that *G. fuliginosa* considered patches to be the unit of available resources. The evidence suggests the species did not generalize their use of these as food availability declined. This result is inconsistent with the prediction from optimal foraging theory.

Explanations and alternatives

If finches selected foods on the basis of profitability of patch types, why did they not generalize their use of these as food levels declined? One explanation is that intraspecific competition for patches was relatively constant among periods. Parker and Stuart (1976) considered that the optimal choice of resource patches will be dependent upon both intrinsic patch value and the amount of extant competition for the resources within that patch. Competition will force exploiters to feed in patches of less intrinsic value (the model is similar to the habitat selection models of Fretwell and Lucas [Fretwell 1972] and Brown [1969]). Thus, if intraspecific competition is approximately constant among seasons, then patch use may not be expected to vary.

Though I cannot say whether intraspecific competition for patches changed or did not change among seasons, this hypothesis seems an unlikely explanation. Actual interference among foraging birds is uncommon; chases are infrequent and only the smallest and most rare patches could be monopolized by individual birds for any length of time. In the present study rare patches were the least profitable ones. Moreover, if it was intraspecific resource competition which caused birds to feed in a wide array of patches we would expect the net gains in each patch type to be essentially identical within a given grid and period (Whitham 1980), and the total quantity of food per bird to be approximately equal in all periods. This was manifestly not the case here (Table 5 and Appendix).

A second possibility is that nutrient differences among seeds of various patch types played a larger role in determining preference than was assumed. An obvious difference among seed types was their size, and hence energy content. However, seeds in general may vary with respect to a host of nutrient classes (e.g., Willson 1971). Should energy content be only one of several determinants of patch choice, the foods would not have been completely substitutable (Rapport 1971) and the predictions from foraging theory would not be expected to apply. Furthermore, the nutrients that determine food preference could differ among seasons, as a result of variation in the physiological and physical condition of the birds. Indeed energy may be a more important determinant of finch survival when food is scarce than when food is abundant, relative to other nutrients. This may explain why profitability (biomass) was a slightly better predictor

of diet when food was scarce than when food was abundant (Table 7).

A third explanation is that optimal foraging theory may not predict a large diet shift when food becomes scarce. Indeed MacArthur and Pianka (1966) noted that if both within-patch search times for items and the time spent between patches declined, their model could not unambiguously predict generalization in patch use. Generalization is expected only if search time within patches declines conservatively with respect to between-patch time. This condition seems provided here (Table 5). However, to determine the extent of generalization that would be expected, changes in the ratio of between-patch to within-patch feeding times must be known. It is not clear that if these values change (as they doubtless have done) that the predicted difference in patch selection would be large and hence detectable with the methods used in this analysis. This aspect requires investigation.

Finally, a tempting hypothesis is that finches employed a more large-scale definition of a "patch" than runs of seeds of a given type. A test of this possibility would require more detailed information on space use and sequences of items in the diet of foraging birds than I currently possess. Parts of the study grids on Pinta tended to attract more birds than other areas but this may have been a consequence of patch choice (as defined herein) rather than a result of a larger scale definition. Undoubtedly the foraging individual perceives the habitat as a hierarchy of levels of "patchiness," but the importance of each level in determining local diet is unknown.

What alternatives to optimal foraging theory might account for the absence of diet generalization in *G. fuliginosa*? A reasonable hypothesis is that it makes little difference to the birds whether or not they forage optimally when food is abundant. Models of optimal diet generally assume that, if it requires time to perform activities other than feeding, then natural selection will inevitably modify behavior to make maximally efficient use of the time actually spent foraging (e.g., Pyke et al. 1977). This need not be the case. When ample resources are available and only a fixed amount is required to satisfy daily demands, then predators may be more careless in their choice of foods. Clearly, if the feeding time required to meet these daily demands is short, or if competing demands on the time budget are few, then there may be small selective reason to minimize feeding times further. Wiens (1976) has forwarded a similar view. Indeed, Hainsworth and Wolf (1979) have argued that at high nectar availabilities random and nonrandom foraging by hummingbirds could result in comparable time budgets. The fact that finches did not generalize their diets may indicate that when food was abundant they chose a diet that was "adequate" rather than optimal.

Given a predator in a field situation, it would be difficult to distinguish whether its diet was optimal or

adequate. However, while the optimal strategy would result in the most efficient diet in all circumstances, the adequacy hypothesis predicts that efficiency will vary with circumstance. Specifically, if an organism suffers no penalty in fitness by deviating from the optimum, then that organism will be no more likely to feed at that optimum than some distance from it. An adequate diet is one which falls within this range of behaviors of equal fitness. This range should constrict as resources decline, and the foraging behavior should more closely approach the optimal solution as a consequence.

Thus, "adequate foraging" predicts that the finches' feeding behavior will vary depending upon the extent to which efficient foraging is necessary. Indeed the hypothesis predicts that if foods are substitutable (Rapport 1971), then profitability should more strongly determine diet choice when food abundance decreases, whereas optimal foraging predicts the opposite trend. Data presented in Table 7 support the adequacy hypothesis: the size and significance of the standard regression coefficients of diet on patch profitability indicate the slightly greater importance of patch profitability toward the end of the study (period D). The coefficients in Table 7 are not significantly different from one another, despite the trend, so the conclusion regarding the change in the predictive capacity of patch profitability is only suggestive. Nonetheless the adequacy hypothesis remains a testable alternative to optimal foraging theory.

A second alternative hypothesis to explain why finches did not generalize their diets is that they could not do so. The finches seemed able to select the seed and patch types of highest reward despite the apparently complex structure of the environment. It may be that this discrimination is the result of a large repertoire of foraging "rules" (e.g., Bobisud and Voxman 1979, Waage 1979) which, though reliable, are relatively inflexible. Differences among organisms in their choice relative to reward in experimental learning situations are known (Shimp 1969, Bitterman 1975) and provide evidence that limitations exist. In a simple patchy environment birds have been shown to modify their behavior in response to increased travel time between patches (Cowie 1977). Whether they would be able to do so when food patches are ill-defined, diverse in type, variable in profitability within a type, and variable in size and profitability among seasons is worthy of study.

In sum, finches selected seed and patch types estimated to yield the highest biomass intake per unit time. Search times between items may increase or decrease the profitability of patch types, in a manner not reflecting the handling efficiency of finches on corresponding seed types. Ground finches generalized to some extent their use of seed types as food abundance declined, but this trend was probably a consequence of selection for profitable patch types. Finches did not

generalize their use of patch types. The first result (food selection) confirms a prediction of optimal foraging models. The second result (seed and patch relations) warns against incautious use of the assumption that environments are fine grained. The third result (diet generalization) contradicts expectation and hence raises questions about the ability of current optimal foraging theory to predict relations between diet and food abundance in nature. It is possible that finches do not always forage optimally, for reasons of behavioral limitations, lack of necessity to forage more efficiently, or both.

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APPENDIX

Mean profitabilities of patch types in grids 1 and 2 for *G. fuliginosa*. — indicates no estimates available.

Plant species	Seed depth (mm)	Profitability (mg/s)					
		Grid 1			Grid 2		
		B	C	D	B	C	D
<i>Eragrostis ciliaris</i>	.18	.0027	.0027	.0027	—	—	—
<i>Aristida repens</i>	.33	.0449	.0449	.0186	.0449	.0449	.0306
<i>Trichoneura lindleyana</i>	.35	.0695	.0695	.0288	—	.0675	—
<i>Coldenia darwinii</i>	.36	—	.0364	.0364	—	—	—
<i>Bouteloua disticha</i>	.47	.1001	.0590	—	.1100	.0590	—
<i>Chamaesyce punctulata</i>	.48	.1146	.1028	.0906	—	—	—
<i>Cyperus andersonii</i>	.57	.0759	.0759	.0376	.0759	.0072	.0365
<i>Portulaca</i> sp.	.63	.1555	—	—	—	—	—
<i>Alternanthera filifolia</i>	.73	.0410	.0504	.0275	.0778	.0289	.0160
<i>Acalypha sericea</i>	.73	—	—	—	.0700	.0176	.0216
<i>Setaria setosa</i>	.74	.1834	—	—	.1425	.1425	.1155
<i>Polygala galapageia</i>	.80	.1534	—	.0441	—	—	—
<i>Paspalum galapageia</i>	.98*	.1729	—	—	.1729	.1781	.1246
<i>Salvia occidentalis</i>	1.00	—	—	—	.0568	.0568	.0629
<i>Boerhaavia caribaea</i>	1.08	.3365	—	—	—	—	—
<i>Alternanthera echinocephala</i>	1.00	—	—	—	—	—	.0624
<i>Scaevola incisa</i>	1.24	.0864	.0684	—	.0950	.0996	.0908
<i>Heliotropium angiospermum</i>	1.51	.1515	.1515	.1144	—	—	.3055
<i>Rynchosia minima</i> †	2.45	.8874	.3376	—	.5767	.4302	.5489

* Depth is 1.00 mm in grid 2.

† Green fruit.