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DETERMINANTS OF MORPHOLOGICAL PATTERNS IN COMMUNITIES OF DARWIN'S FINCHES

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Lack's (1947) comparative study of Darwin's finches led him to two influential conclusions concerning the processes that shape morphological properties of species communities. First, he stressed the adaptive nature of much of the morphological variation among populations and species, particularly in relation to diet. Second, Lack argued that morphological differences between species were frequently a consequence of competition for food resources. Such differences arose in two ways: (1) by the extinction of species morphologically (and hence ecologically) similar to others, and (2) by natural selection causing morphologically similar species to diverge. The former process is competitive exclusion; the latter is character displacement. As a result of these claims and Lack's evidence to support them, Darwin's finches have become a classic example of the workings of natural selection, and of the general influence of interspecific competition on morphological patterns in species communities (Grant 1981*b*; Sulloway 1982).

These views have been challenged from several sources. Bowman (1961) pointed out that the Galápagos islands are floristically different from one another, a fact later confirmed by Abbott et al. (1977). He argued from this and other considerations that floristic diversity was the most important determinant of morphological patterns. Strong et al. (1979) and others (Simberloff 1978; Connor and Simberloff 1978) also criticized Lack's evidence for competitive exclusion and character displacement. These authors showed that morphological and distributional patterns of the finches do not differ significantly from patterns in hypothetical communities produced by randomly combining species. They also rejected Bowman's food supply arguments, and Abbott et al.'s modification to include effects of both island food supplies and interspecific competition, in favor of a hypothesis that present-day properties of Galápagos bird communities are primarily the result of "random processes" (Strong et al. 1979).

Similar arguments apply to patterns in other species communities, not just Darwin's finches (e.g., Ricklefs and Travis 1980; Simberloff and Boecklen 1981), and reflect a wide diversity of opinion about probable causes of morphological

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patterns. The arguments have been difficult to settle primarily because data to evaluate alternative explanations are usually unavailable, and because the means to do so are often equivocal. This latter criticism applies to the modern technique of comparing actual communities to randomized communities in order to detect the effects of competition (Grant and Abbott 1980; Gilpin and Diamond 1982; Grant and Schluter 1983; Colwell and Winkler 1983), as well as to the more traditional methods of comparing populations in sympatry with those in allopatry, or mainland and island communities (Connell 1975; Simberloff 1978).

Our contribution here is the development of a procedure which overcomes many of these difficulties. The procedure is used to evaluate alternative explanations for morphological patterns in *Geospiza*, the Galápagos ground finches. The key feature of the procedure is a quantitative representation of environments in terms relevant to the differential persistence of morphological forms. Our initial premise is that food characteristics are potentially the most important determinants of finch morphology on Galápagos islands. This premise is not unreasonable: detailed field studies have documented very significant effects of food on the diet, distribution, abundance, and differential survival of ground finches (Abbott et al. 1977; Smith et al. 1978; Grant and Grant 1980*a*, 1980*b*; Boag and Grant 1981; Grant 1981*a*; Grant and Grant 1982; Schluter 1982*a*, 1982*b*; Schluter and Grant 1982; Price and Grant 1984).

The procedure estimates the abundance of a colonizing finch species on islands in the absence of interspecific competition. Three steps are involved. First, the range of seeds that a hypothetical species may consume is determined; this range is constrained by the mean phenotype of the species. Next, for each Galápagos island the combined abundance of all available foods lying within this range is determined. Finally, the number of individual finches that may be supported by this quantity of food is computed. The procedure is repeated for all feasible morphologies. The result, for each island, is a curve giving the expected population density of a solitary finch species as a function of its mean phenotype.

The new variable "expected population density" is of interest for two reasons: (1) the probability of successful island colonization by a species may be related to its population size (MacArthur 1972) and (2) natural selection, acting on individuals, is expected to modify the mean phenotype of a solitary species with the result that population size is approximately maximized (Roughgarden 1976). Expected density curves thus allow us to make predictions about morphological patterns from models assuming different causes. Models are then compared in terms of the accuracy of their predictions.

For reasons discussed later, this analysis is restricted to generalist granivores within the *Geospiza*.

MODELS

Five models were tested. They differ in the extent to which the evolution and/or assembly of species is directed by food supply, through its effects on population density, and by interspecific competition for food. Assembly refers to the processes of colonization and extinction which determine the combination of species present on an island.

1. *Undirected assembly/evolution.*—Food supply limits the range of feasible morphologies, without influencing the probability of persistence or evolution within this range. Interspecific competition is absent.
2. *Partly directed assembly.*—Food supply influences the probability of persistence of morphological forms. This probability favors species in proportion to their expected population size; interspecific competition is absent.
3. *Directed evolution.*—Natural selection guides the mean phenotypes of species to correspond to local maxima in expected population size, as determined by food supply. Interspecific competition is absent.
4. *Directed assembly with competitive exclusion.*—Species compete for available foods, and so each modifies the expected population density of the others. Food supply influences the outcome of competition by consistently favoring the species with greater expected population size. Morphology of species is assumed fixed and does not evolve.
5. *Directed coevolution under interspecific competition.*—Phenotypes of competing species coevolve to maximum population sizes, as determined by food supply and modified by competition.

A distinction is made between evolution and coevolution. Evolution refers to general morphological adjustments by species, while coevolution refers only to morphological adjustments in response to competitor species. Coevolution is a more general term than character displacement, encompassing divergence as well as the prevention of convergence.

DATA

Construction of expected population density curves, and subsequent tests of models, requires information on food supply. Additionally, we require quantitative knowledge about how the range of foods eaten is influenced by morphology, and how food supply within this range affects finch abundance. The relevant empirical information is summarized below.

Food Supply

Abundance of foods was determined by random sampling procedures in selected sites (Abbott et al. 1977; Schluter 1982*a*). Food supply data are available for 15 islands visited at least once between 1972 and 1981 (Appendix). Where possible, late dry season information was used (September to early January), when foods are most likely to be limiting (Smith et al. 1978; Grant and Grant 1980*b*; Schluter 1982*a*, 1982*b*). For three islands we have been forced to use data from the late wet/early dry season (March to June). The results are not highly sensitive to seasonal variation in food supplies, as indicated by analysis of five islands visited in both these periods. Annual variation in food supplies is another potential problem, though data collected from three islands in both 1973 and 1979 or 1981 (Genovesa, Daphne, and Española) gave consistent results between years.

Finch Species

This study is concerned with morphological patterns in the generalist granivores, those *Geospiza* populations which feed almost entirely on seeds in the dry season (Appendix). Excluded are *Geospiza* populations which have specialized habitat requirements, or which take seeds only infrequently. This is done for practical reasons: it is difficult to describe resource variables when habitat restrictions are involved, and it is difficult to compare the abundance of important habitat variables to the abundance of seeds. Also, use of different microhabitats is not simply predicted by morphology (e.g., D. Schluter and P. R. Grant, MS) whereas use of seeds usually may be predicted (Abbott et al. 1977; Grant 1981*a*; Schluter 1982*a*, 1982*b*). Doves are also excluded, the only major non-*Geospiza* granivore. While little quantitative information exists on their habits, doves are known to feed very differently than finches, and often take different seed types (e.g., Grant and Grant 1979). Later, the influence that habitat specialists and doves may have had on community organization in the generalist granivores is discussed.

All populations of *G. fuliginosa, G. fortis,* and *G. magnirostris* are included in the generalist granivores (e.g., Smith et al. 1978; Schluter 1982*a*), but the *Opuntia* specialist *G. scandens* is excluded. *Geospiza scandens* eats seeds in the dry season on some islands, but it is everywhere a habitat specialist, taking most of its foods from *Opuntia* cactus (Smith et al. 1978; Grant and Grant 1981; Millington and Grant 1983). Its presence and local distribution on islands is determined by *Opuntia*. *Geospiza conirostris* on Genovesa is also an *Opuntia* specialist, while the same species on Gardner and Española is a generalist granivore (Grant and Grant 1982).

Populations of *G. difficilis* on islands with a highland zone are also excluded from the analysis (Pinta, Santiago, and Fernandina). These forms restrict their foraging effort to areas of deep ground litter; here they may take seeds, but more commonly they consume invertebrates (Schluter 1982*a*; D. Schluter and P. R. Grant, MS). *Geospiza difficilis* populations on low, dry islands consume mainly seeds, and do not show any such microhabitat restriction (Schluter and Grant 1982, MS); hence they are included.

Morphology and Diet

The beak is the finch's chief instrument for acquiring, manipulating, and crushing seeds. Hence the dietary significance of interspecific variation in beak size, specifically depth, is considered for reasons discussed in Abbott et al. (1977) and Grant (1981*a*). Other beak size variables are correlated with this dimension, as is body mass (fig. 1).

Figure 2*A* shows that the hardest seed preferred by finches is a positive function of beak depth (log (base *e*) transformed data; $r = .97$, $P < .001$). Preferred seeds are those whose proportional representation in the diet is at least 50% greater than their proportion in the environment (Abbott et al. 1977). Observation suggests that the finches are largely incapable of cracking the harder seeds available (fig. 2*A*;

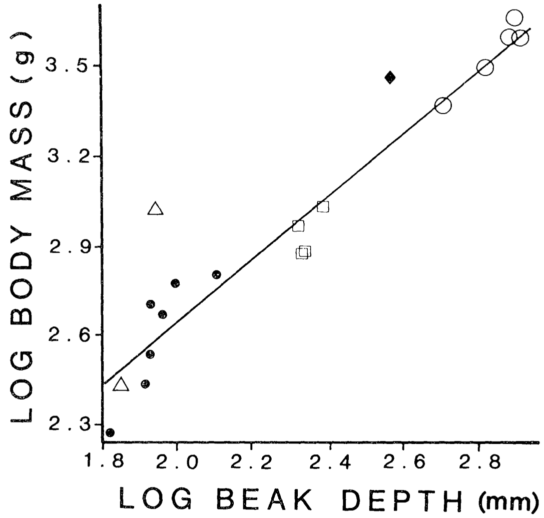

FIG. 1.—Allometry between body weight and beak depth (natural logs) in adult male finches. Symbols: *Geospiza fuliginosa* (●), *G. fortis* (□), *G. magnirostris* (○), *G. difficilis* (△), and *G. conirostris* (◆). Linear regression ($Y = 1.1X + .49$) was computed using only *G. fuliginosa*, *G. fortis*, and *G. magnirostris*, and is highly significant ($r = .98$, $P < .001$).

Schluter 1982*b*). Seed size is correlated with hardness (Abbott et al. 1977), but the latter variable is the most likely limiting factor. For example, *G. fuliginosa* commonly opens the large soft fruits of *Rynchosia minima*, but it cannot usually crack the smaller, harder *Lantana peduncularis* seeds (Schluter 1982*b*).

There are gaps in the frequency distribution of seed hardnesses (fig. 2*A*), so the hardest seed preferred by a species is not necessarily the hardest one that could be eaten, if available. The procedure for constructing density curves thus uses the dashed line in figure 2*A*, 1 SD above the line of best fit, as an estimate of the upper limit to this capacity. One point is not included by this bound (*G. conirostris*); possibly this species can crack harder seeds than expected because of greater skull and beak musculature, as indicated by its proportionately large body (fig. 1).

The lower bound to the preferred range of seeds is more likely to be determined by seed size than hardness. Smaller seeds are relatively less profitable for large finches than for small finches, and are hence more likely to be ignored (Schluter 1982*b*). Figure 2*B* illustrates this relationship. While the two variables are correlated ($r = .89$), a curvilinear relation is suggested by the data. Log depth of the smallest preferred seed was therefore described as a nonlinear function of log beak depth, estimated using an iterative program in BMDP(3R). Before fitting, the outlier *G. magnirostris* on Wolf (z) was deleted from the data set, because it prevented convergence to the same solution for different initial parameter values. The position of this outlier can be explained by a large gap below it in the frequency distribution of available seed sizes on that island. To correct for such gaps in general, the dashed curve in figure 2*B* is employed as a conservative estimate of the lower bound to the preferred range.

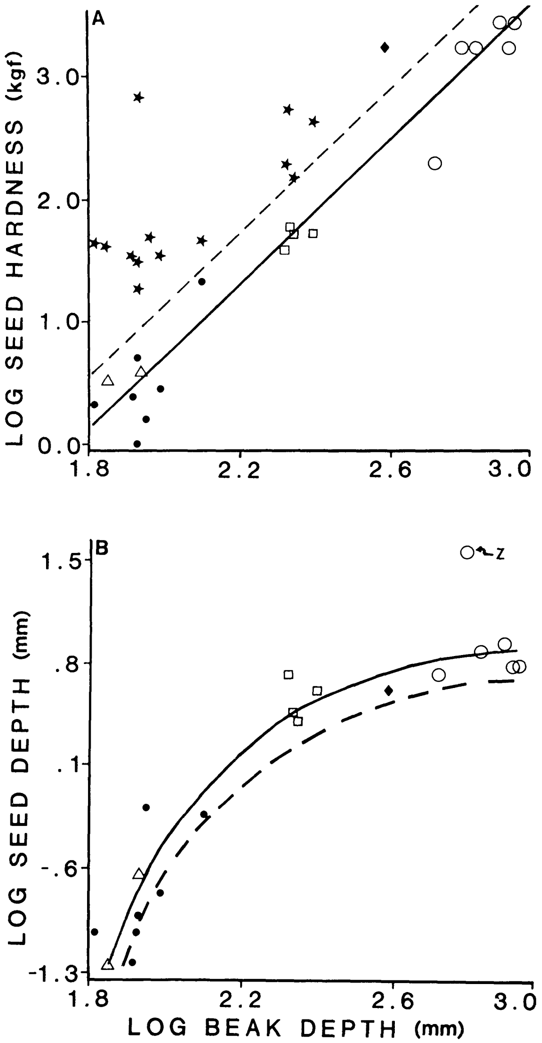

FIG. 2.—*A*, Mean hardness (kgf) of hardest seed preferred regressed against mean beak depth of adult male finches. Linear regression uses log-transformed data; $Y = 3.0X - 5.3$. Dashed line adds 1 SD of the residuals to Y. Stars show hardness of seeds not consumed by these populations. Symbols as in fig. 1. Hardness was determined using the McGill seed-cracker (Abbott et al. 1977). *B*, Mean depth (mm) of smallest seed preferred in the dry season, regressed against mean beak depth of adult males. Nonlinear regression uses log-transformed data, and excludes the outlier (z); $Y = 1.0 - 472\exp\{-2.9X\}$. Dashed curve subtracts 1 SD of the residuals from Y. Seed depth is the intermediate of the three dimensions L × D × W.

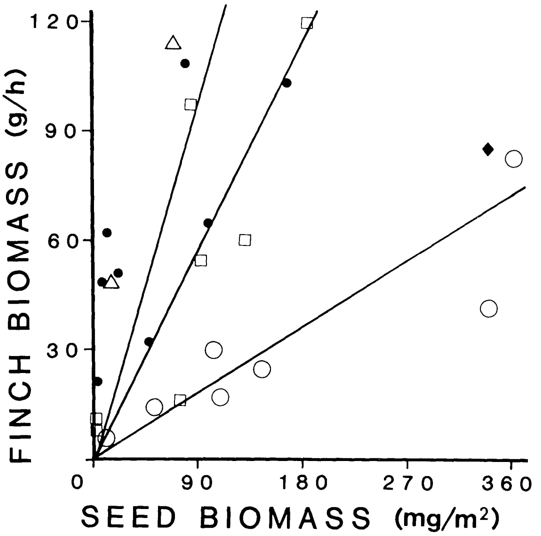

FIG. 3.—Number of finches encountered per hour in census walks, converted to biomass, plotted against the biomass density of preferred seeds. All points are from the late dry season. Regressions are for *G. fuliginosa* (●), *G. fortis* (□), and *G. magnirostris* (○). The predictive relationships are summarized by the equation $Y = AX$, where $A = 1.9 - .62$ log beak depth. Other symbols as in fig. 1.

Finch Density and Food Supply

A relationship between finch density and food supply remains to be determined. An empirical relationship was used, derived from dry season data, shown in figure 3. Density estimates are based on census walks (Schluter 1982*a*). Values are unweighted averages over sites, converted to mass units for easier interspecific comparison. In a few cases density data are available only from mist-netting censuses (e.g., Smith et al. 1978). Since results of the two census methods are highly correlated (Schluter 1982*a*), netting totals were converted directly onto the census walk scale.

Food supply refers to the abundance of preferred seeds averaged over sites on a given island (fig. 3). This includes most but not all seeds falling between the upper and lower size-hardness limits for a given beak size (fig. 2). A number of ripe seed types are virtually ignored by finches whenever they are encountered, yet there are no mechanical reasons for this (Grant and Grant 1980*a*; Schluter 1982*b*). These constitute all available seeds of the Malvaceae, Convolvulaceae, and Rubiaceae, and almost all the Leguminosae. There is reason to suspect that the ripe seeds are toxic to finches (e.g., Janzen 1981), and so they are excluded from this and all subsequent analyses.

A wide scatter of values results in figure 3, but points for different species tend to occupy different sections of the figure. Regressions confirm this: slopes for *G. fuliginosa, G. fortis,* and *G. magnirostris* were computed using a fixed zero-intercept model, with the variance in Y assumed proportional to X. All slopes are significant ($P < .05$). Residuals indicated the need for a weighted regression model

(Neter and Wasserman 1974). However, the variances of the weighted deviations from regressions are extremely heterogeneous, preventing a comparison of slopes using ANCOVA. The unweighted regression slopes are similar to the weighted slopes, and are significantly different from one another ($P < .05$).

There is a pattern to the different slopes: the largest species (*G. magnirostris*) has the lowest slope, and the smallest species (*G. fuliginosa*) has the highest. Other species conform to this pattern: *G. difficilis*, similar to *G. fuliginosa* in size, has values near the *G. fuliginosa* regression. Española *G. conirostris*, similar to *G. magnirostris* in size, occurs near the *G. magnirostris* regression. The procedure for constructing density curves preserves the differences in slope among species of different size (fig. 3). While this is not essential, since a slope formed by averaging the three slopes gives similar final results, correcting for finch size provides a more realistic estimate of expected population densities than does average slope. Magnitude of slopes in figure 3 are inversely correlated with average log beak depth of populations ($r = -.998$, $P < .05$, $n = 3$); this is the linear correction employed.

EXPECTED POPULATION DENSITY ON ISLANDS

The previous relationships allow the construction of curves describing expected population density of a solitary finch species as a function of the mean size of its beak. Table 1 gives a demonstration of the calculations involved. For a given beak depth the preferred size-hardness range of seeds is determined using the relation in figure 2. Those seeds on the particular island which fall between these limits are identified and their biomass is summed. Seed biomass is converted to finch numbers using the results of figure 3 and the known mass of individual finches of a given mean beak size (fig. 1). This procedure is repeated for the entire feasible range of beak depths, for all islands. The results, in log beak depth increments of .05, are given in figure 4.

The lowest beak depth in figure 4 was set by practical limitations: the apparatus for determining seed hardness (Abbott et al. 1977) cannot record values below about 1 kgf, approximately the upper seed hardness limit for a beak of log depth 1.7 (5.5 mm). This value is a reasonable minimum depth, as it is smaller than the mean beak depth of any *Geospiza* (fig. 1). Additionally, the smallest granivores in this hemisphere (e.g., *Sporophila minuta* and *Volatinia jacarina*) have a body mass of at least 8 g (R. W. Storer, personal communication). For *Geospiza* this weight corresponds to a log beak depth of about 1.5 (fig. 1), a value close to the actual lower limit (fig. 4). The maximum beak depth value is set by empirical constraints: given the relationship between slope and beak depth in figure 3, a finch of log beak depth greater than 3.2 (24.5 mm) cannot have positive density. This maximum is also reasonable: It is larger than that of any Galápagos finch, and it corresponds to a body mass of about 50 g (fig. 1), a mass exceeded by few granivorous passerines (R. W. Storer, personal communication).

The most striking feature of these curves (fig. 4) is that they are not normal, as is commonly assumed in theoretical treatments of environments (e.g., MacArthur 1972; Lande 1976; Roughgarden 1976; Slatkin 1980). In fact most of the curves are

TABLE 1

CALCULATION OF EXPECTED POPULATION DENSITY AS A FUNCTION OF BEAK DEPTH FOR ISLA WOLF

SEED TYPE	LOG SEED HARDNESS (kgf)	LOG SEED SIZE (mm)	LOG BEAK DEPTH															
			1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0	3.1	3.2
1.	≤.0	−1.38	X	X														
2.	≤.0	−1.20	X	X														
3.	≤.0	−.69	X	X	X	X												
4.	≤.0	−.46	X	X	X	X												
5.	≤.0	−.22	X	X	X	X	X											
6.	.69	1.00			X	X	X	X	X	X	X	X	X	X	X	X	X	X
7.	2.83	1.57										X	X	X	X	X	X	X
8.	3.21	1.90												X	X	X	X	X
Food biomass (mg/m^2).			25	25	66	66	42	41	41	41	41	103	103	306	306	306	306	306
Finch biomass (mg/h).			23	21	51	47	27	24	22	19	17	35	29	66	47	28	9	0
Expected density (no/h).			6	5	11	9	5	4	3	2	2	4	3	6	4	2	1	0

NOTE.—Only 8 edible seed species were present. Symbol 'X' indicates those seeds which lie between the size-hardness limits for a finch species of given mean beak depth (fig. 2). Food biomass is the summed density of seeds so indicated. This is converted to finch biomass using the results of fig. 3. Biomass is converted to expected (numerical) density using the results of fig. 1. This example uses log beak depth increments of .10; the results in increments of .05 are plotted in fig. 5. Seed species are in order: *Mollugo, Eragrostis, Portulaca, Cyperus, Alternanthera, Croton, Opuntia,* and *Cenchrus*.

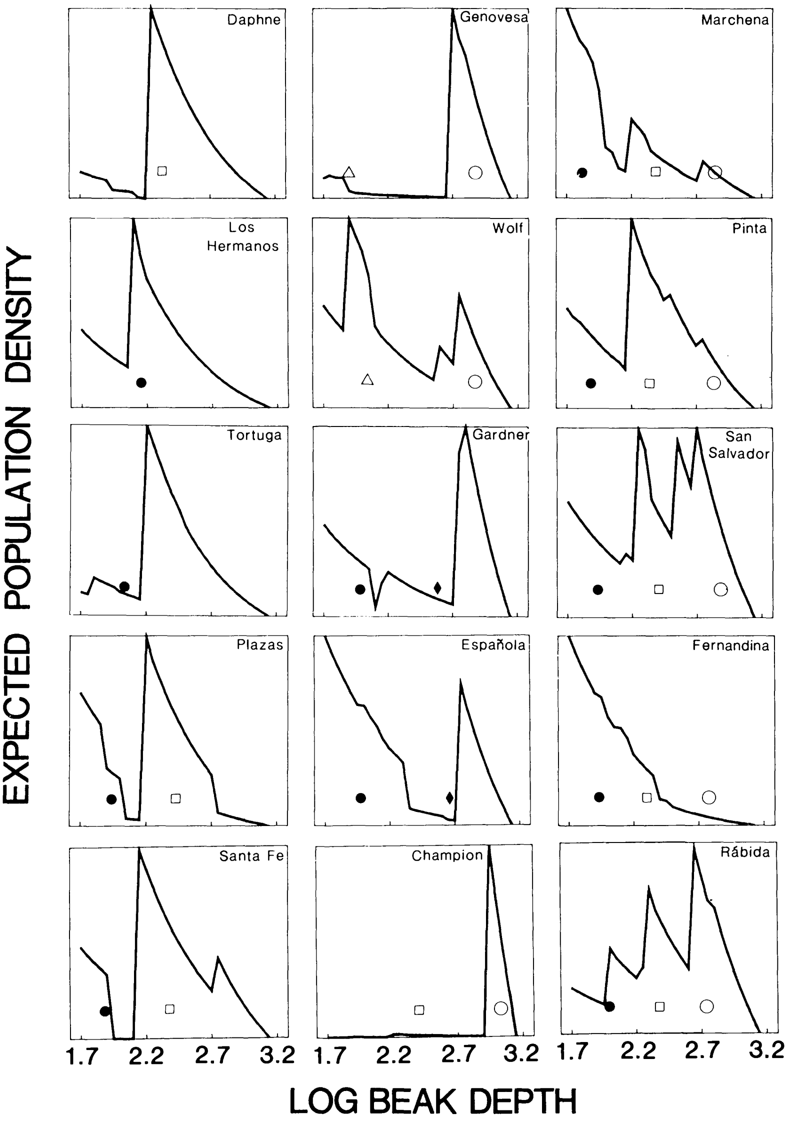

FIG. 4.—Expected population density of a solitary granivorous finch species on 15 Galápagos islands, as a function of beak depth. Absolute heights of curves are scaled and are not comparable between islands. For example, the small local maximum at an intermediate beak depth on Champion is absolutely higher than any of the Rábida maxima. Mean log beak depths of actual populations (adult males) are indicated for each curve. Species symbols are as in fig. 1. Beak depth for Champion *G. magnirostris* is based on Lack's (1947) measurements of "Darwin's" *G. magnirostris*.

not even unimodal, or symmetric. Instead expected density is usually a polymodal function of beak depth.

A second feature of these curves is the variation among islands in the shape of the density function. A few curves possess only one local maximum, but most have several, and the position and breadth of maxima are variable. This variation is entirely a consequence of interisland differences in food characteristics.

These two features have important consequences for the prediction of morphological community patterns, discussed next.

PREDICTIONS OF MORPHOLOGICAL PATTERNS

Model I: Random Assembly/Evolution

The simplest effect of food supply could be to set just the limits to the feasible range of mean beak sizes. By model I all phenotypes are equally likely to successfully colonize or evolve where expected population density is positive; competition and variation in food supply play no role. For most islands this includes all values between 1.7 and 3.2 (fig. 4). In two cases (Santa Fe and Daphne) there is a short gap between these bounds.

If all forms are equiprobable, then the mean phenotype of a species should be distributed as a uniform random variable between these limits. This prediction is tested in table 2, which shows the smallest difference, d, between adjacent species on islands where at least two species are present. Under model I the probability (P) that the minimum difference is at least as large as the observed d is

$$[1 - (N - 1)d/1.5]^N$$

(e.g., Ross 1976), where N is the number of species present. A slightly modified form of this equation was used for Santa Fe, taking into account the gap in the density function.

In most cases the calculated probability is small, especially for three-species islands (table 2). In all cases P values are less than .53, a result not expected under model 1. Species are thus much more widely spaced along the morphological gradient than predicted by this model.

Model II: Partly Directed Assembly

In model II, unlike I, food abundance influences the probability that a species of given mean beak depth will be present, within the feasible range. This assumes that a species with high population density will be more likely to persist than a species with low density. The probability of success is here assumed to be proportional to the expected density (fig. 4). Interspecific competition again has no effect.

Model II was tested using random simulation. N hypothetical species were thrown 100 times onto each island, where N is the number of species actually present. In each of the 100 cases species were randomly and independently assigned a mean beak depth. Thirty-one beak depth values were possible, representing increments of 0.05 between the limits 1.7 and 3.2. The multinomial

TABLE 2

ASSESSMENT OF THE ABILITY OF MODELS I, II, AND III TO ACCOUNT FOR MORPHOLOGICAL DIFFERENCES BETWEEN SPECIES

ISLAND	NO. GRANIVORE SPECIES	MINIMUM d	PROBABILITY (P)		
			I	II	III
Pinta	3	.43	.08	.02	.00
San Salvador	3	.47	.05	.01	.09
Fernandina	3	.39	.11	.02	.00
Rábida	3	.37	.13	.15	.09
Marchena	3	.48	.05	.06	.22
Genovesa	2	1.03	.10	.11	.00
Santa Fe	2	.48	.47	.46	.44
Plazas	2	.41	.53	.45	.50
Champion	2	.68	.30	.00	.38
Española	2	.63	.34	.34	.50
Gardner	2	.56	.39	.45	.22
Wolf	2	.85	.19	.16	.22
Combined probabilities (P')			.0010	.0002	.0005

NOTE.—d is the smallest difference in log beak depth between species on islands, P is the probability under each model that a value as large as d could be produced by chance. If the model is correct, the 12 P values should be uniformly distributed between 0 and 1. This is tested using the combined probability (P') under each model of recording no P value greater than the largest value observed (P_{max}, underlined): $P' = 2(P_{max})^{12}$ (two-tailed test).

probability that a particularly beak depth was assigned is given by the scaled height of the density curve at that point (fig. 4). For example on Santa Fe a finch species of log beak depth 2.15 is more probable than any other beak size, and has about twice the probability of being present as a finch of beak 1.7.

Table 2 compares simulated and actual communities in their morphological differences between species. P values are the proportion of times that the minimum difference between adjacent species in simulated communities was as great or greater than the observed d. Because only a discrete number of values was used in the simulation, the observed d was rounded off to the nearest .05 before comparison. Again the observed d is improbably large in most cases, especially for three-species islands. All P values are less than .46, an improbable event under model II.

Model III: Directed Evolution

Under model III, only beak sizes corresponding to "peaks" in expected population density are possible (fig. 4). This assumes that natural selection will invariably shift the mean phenotype of successful colonists to points which maximize local population density. Each species evolves independently of the others: competition is assumed to be absent. A peak is here defined by any local maximum along the morphological gradient where expected density is greater than the density at points up to .10 units away (2 increments of .05). For example Pinta has two peaks and San Salvador has four (fig. 4). This definition assumes sufficient morphological variation in each population to bridge more narrow local maxima.

Data in table 2 test this model. For simplicity, the test assumes that all phenotypes defining peaks in expected density are equiprobable. Since peaks are few in number, all possible beak depth combinations could be listed for each island. *P* was then computed directly as the fraction of combinations where the minimum difference exceeded the observed *d*. Like earlier models, III does not satisfactorily account for observed differences between species. This is primarily because in randomly assigning species to peaks there is a high probability that two will be assigned to the same peak, resulting in a minimum difference of zero. This is necessarily the case on islands where there are fewer peaks than species present (e.g., Pinta and Fernandina). Even where there are at least as many peaks as species, the probability of a nonzero value for *d* is small (e.g., Marchena, $P = .22$). Figure 4 shows that observed phenotypes do correspond to the position of peaks in the expected density curves, on islands where such peaks are present. However, two species never occupy the same peak, or peaks very close to one another. This is not expected by chance (table 2).

Note that the above definition of a peak is conservative: there may be enough morphological variation in some populations to bridge even wider local maxima (Grant and Price 1981). A more stringent definition reduces the number of peaks on islands and increases the probability that zero minimum differences will occur, under model III.

Model IV: Directed Assembly with Competitive Exclusion

Previous models were unable to account for large differences between species, suggesting that interspecific interactions may have influenced morphological patterns. Model IV assumes that communities are assembled under interspecific competition for food. It differs from previous models in that the expected density of each species on an island is modified by the presence of other species, to the extent that it may become extinct. For simplicity, species are assumed not to evolve once they have colonized.

A test of the model required simulation of a colonization process with competitive exclusion. Three species with beak depths given by three of the 31 possibilities between 1.7 and 3.2 were allowed to colonize a given island (fig. 4). The conditional expected population density of each was then computed as its expected density excluding all foods lying within the preferred range of any of the other species on that island (fig. 2). The process determined those species whose conditional density was zero, and caused the extinction of the one with the lowest expected density. Conditional densities were then recomputed for all remaining species. This extinction procedure continued until all remaining species had positive conditional density. A new colonist was then added, and the entire process repeated, until no additional morphological form could successfully invade.

This version of model IV basically demands as a condition for coexistence that all species present on an island have access to at least one available food not in the preferred range of any other species present (e.g., Schoener 1976). Food abundance plays an additional role by determining the species of greatest density, when more than one species utilizes an array of foods. Unlike previous models the

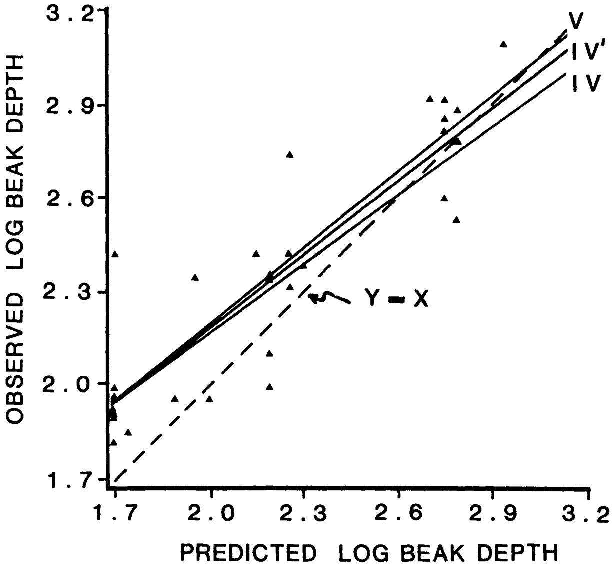

FIG. 5.—Observed morphology of species regressed against predicted morphology, under models IV, IV′ and V (solid lines). Data points are illustrated for only the model IV′ case, but their arrangement is highly consistent in all three cases. Regression formulas are $Y = .75X + .66$ (model IV), $Y = .80X + .59$ (model IV′), and $Y = .83X + .54$ (model V).

procedure is completely deterministic, producing for a given island the same result regardless of the order of colonization of morphological forms. It can thus be used to predict precisely the phenotypes present on any island.

For four islands (Genovesa, Tortuga, Los Hermanos, and Daphne) the model predicted one more species than is present. The species with the lowest conditional density was therefore deleted from each of these islands before the test. For three islands, Marchena, San Salvador, and Rábida, model IV predicts that only two species can coexist, whereas three are actually present. These three islands were of necessity excluded from the first test of model IV.

For the 12 included islands, the relation between morphological patterns predicted by model IV and those observed is shown in figure 5. Data points for the regression were derived by matching observed and expected phenotypes on each island on the basis of rank position. That is, the predicted beak size of the *n*th smallest species observed on any island is the beak size of the *n*th smallest species predicted by the model. The resulting correlation between observed and predicted morphology is high ($r = .90$, $N = 23$).

The data points are not completely independent, since morphologies are ranked within islands. To accommodate this, the above correlation was compared with the distribution of coefficients generated by simulations using the three noninteractive ("null") models, I, II, and III. Each simulation involved throwing N hypothetical species once onto each island, where N is the number of species actually present. The probability that a particular beak depth was assigned depended on the model (see earlier). The correlation was then determined between this random morphological pattern and the observed pattern, matching phenotypes within islands on the basis of rank position. This whole procedure was repeated 100 times for each of the three models.

The highest of 300 resulting random correlation coefficients was $r' = .26$. This value is the estimate of the upper critical limit for rejection of the null hypothesis at level .01. Since the observed r is much greater than r' we estimate that $P \ll .01$, regardless which of the three null models is used to test the significance of the correlation. Therefore, model IV explains a very large fraction (81%) of the total variation in mean beak depth among populations and species of granivorous finches, and this fraction is not explained by chance.

The outcome of the model is not highly sensitive to variation in the intensity of competition. A second test of this model (hereafter IV′) relaxed the degree of influence of each species on the others. The procedure was identical to the previous test except that conditional expected density was computed using a narrower seed size-hardness range than the preferred range. Model IV′ elevates the lower limit of the preferred range to 1 SD above the curvilinear regression in figure 2*B*. The competitive influence of each species on others is now restricted to a range of foods closer to the upper hardness limit set by morphology; these are the foods on which a species feeds most efficiently (Schluter 1982*b*). All 15 islands were used in the test of the model since the observed number of species was no greater than the predicted number. For 11 islands one more species was predicted than is observed, and that species with the lowest conditional density was deleted from the simulated communities before the test. Predictions from model IV′ are compared with observed data in figure 5. The resulting correlation is identical to model IV ($r = .90$, $N = 32$) and is estimated to be significant at $P \ll .01$.

The correspondence between observed and expected phenotypes is evident in figure 4. Since the rules which govern community assembly in model IV favor those species with high expected densities, the predicted phenotypes usually occur where the density curve reaches a local maximum, as do the observed phenotypes.

Also evident in figure 4 is the tendency for observed values to be greater than predicted (fig. 5). On most islands the morphologies of species are slightly displaced to the right of the morphologies corresponding to maxima in the density curves (e.g., Genovesa and Marchena). This may be because a larger beak or body enables more efficient exploitation of seeds responsible for maxima (Grant et al. 1976; Boag and Grant 1981; Grant 1981*a*; Schluter 1982*b*), a factor not considered in detail by these models. Two conspicuous exceptions to this rule are *G. conirostris* on Gardner and Española. But this species cracks harder seeds than the hardest assumed for a finch of its size (fig. 2), and actually exploits those seeds responsible for the nearby peaks. Hence its "effective" morphology is actually greater than that observed in figure 4.

Model V: Directed Coevolution under Interspecific Competition

The previous model assembles communities solely through the selective extinction of colonizing forms. In contrast, morphological patterns might result from the coevolution of forms driven by interspecific competition. Model V assembles hypothetical communities on the basis of such a process.

To test the model it is assumed that natural selection adjusts the mean phenotype of a species to maximize its population size, conditional on the morphology of all other species present (Roughgarden 1976). For each island all possible N-species combinations of mean beak depths were listed, where N is the number of species actually present. For each species mean beak depth can assume one of 31 values between 1.7 and 3.2 (fig. 4). Next the conditional density of each species was determined within every possible combination of mean beak depths. Conditional density was computed as in model IV′ because the method yields positive values for at least as many species as are found on each island.

Finally, that combination of beak depths was determined for each island at which the conditional density of each phenotype is maximum, given the beak depths of the other species in that combination. That combination should define the endpoint of a coevolutionary process (see also Case 1979). Multiple solutions may be possible in a few cases where there are more local maxima than species present on an island (e.g., Daphne; fig. 4). For simplicity, no constraining influence of local maxima on coevolution was assumed.

As before, predicted and observed phenotypes were matched on the basis of rank position (fig. 5). Again there is a good correspondence between the two variables ($r = .92$, $N = 32$). Using simulation (see earlier) we estimate $P \ll .01$.

DISCUSSION

The five models contrasted are clearly not equally successful in accounting for morphological patterns in communities of granivorous *Geospiza*. Models I, II, and III assume widely varying degrees of influence of food supply on these patterns, yet each fails to adequately explain morphological differences between species. In contrast, two models assuming effects of interspecific competition in addition to food (IV and V) closely account for observed morphological structure in these communities.

These results provide strong support for Lack's (1947) arguments concerning both the adaptive significance of morphological variation and the importance of interspecific competition in the radiation of Darwin's finches. They also show that Lack underestimated the importance of interisland variation in food supplies. Other studies have made similar interpretations of structure in these finches in specific cases (Abbott et al. 1977; Smith et al. 1978; Grant and Grant 1982; Schluter and Grant 1982, MS). This study shows for the first time that a simple deterministic model incorporating only these two factors can accurately predict observed morphological patterns (see also Case 1979).

Note further that tests of these models assumed morphological patterns to be independently determined on different islands. Additionally, between the limits no restrictions were assumed on the range of mean morphologies available to each island. Actually, all finch species evolved in situ on the Galápagos, and all islands are dependent for colonists on a shared species pool. Thus geographical dependencies and historical limitations on the range of morphological types available for colonization could have influenced observed patterns. Limited amounts of genetic variation within populations could also have curtailed local adaptation in some situations. Given the possibility of such restrictions it is all the more surprising that models ignoring them produce such a good fit to actual patterns. The predictive success of the simple models suggests that the role of these restrictions in the development of finch community structure has been minimal.

While competition is the important feature of models IV and V that distinguishes them from the other models, an important reason for their predictive success is in the shape of the expected population density curves (fig. 4). In particular, the curves are polymodal. Since both evolutionary and colonization/extinction processes are biased in favor of phenotypes with high expected density, each curve essentially describes a complex "adaptive landscape" (*sensu* Simpson 1953; Lande 1976). To our knowledge this is the first quantitative demonstration of polymodal landscapes in nature.

Polymodality is a robust property of these curves, following directly from gaps and irregularities in the frequency distribution of seed size-hardness values (e.g., table 1). Within reasonable limits, altering the relationship between beak size and other variables involved in the computation of expected density (e.g., to accommodate possible effects of current competition on the limits of resource use), only shifts the position and height of local maxima, but does not alter the basic features of the curves.

A consequence of such a landscape, under models IV and V, is the prediction of morphological patterns where phenotypes for individual species correspond closely to the position of local maxima, where these exist. The influence of food supply is thus very specific: interisland variation in the shape of the density curves is responsible for all interisland variation in the predicted patterns of species phenotypes.

In contrast, the influence of competition in these models is very general: species are prevented from occupying the same local maximum, or closely adjacent maxima. This is the main reason why the predictions of model IV are stable under at least some variation in the intensity of interspecific competition (e.g., model IV′).

Polymodality of density curves has some other general consequences. It resolves the problem that character differences among sympatric granivorous finch species are larger than expected from a character displacement model assuming symmetric, normally distributed resource functions (Bulmer 1974; Slatkin 1980). Slatkin showed that the predictions of his model were sensitive to the symmetry assumption. The results of this study suggest that the assumption of unimodality, and indeed continuity, is also unduly restrictive, at least for Galápagos islands.

Where only one granivorous species is present on an island (e.g., Daphne, Los Hermanos), its beak depth usually corresponds to the highest local maximum in expected density. In general, this arrangement may result in a high degree of stability of mean phenotypes in these populations through time, though a high degree of heritable variation in this trait may exist (Boag and Grant 1978). Where more than one species is present the same stability may be expected. Polymodality thus confers a certain degree of independence on each species: to the extent that a local maximum constrains evolutionary change in a population, deletion of an adjacent species should not greatly influence the morphology of the former.

This last point bears on the difficult question of which process, colonization and extinction (model IV) or coevolution (model V), is responsible for morphological patterns in the finches. Other data indicate that competitive exclusion is operating: while morphological structure of communities is predictable, the particular combination of species involved is not (fig. 4). Grant and Grant (1982) and Schluter and Grant (1982) analyzed two replacement patterns in detail, *G. conirostris–G. magnirostris* and *G. difficilis–G. fuliginosa* (e.g., Genovesa vs. Española; see also Case and Sidell 1983; Grant and Schluter [1983] for statistical analyses of replacement patterns). Other evidence for colonization/extinction includes a relationship between species number and resource diversity (Abbott et al. 1977). In the present study the actual number of granivore species on an island is correlated with the number predicted by simulation of model IV′ ($r = .79, P < .01, n = 15$); this predicted number is an indication of the range of resources available.

Strictly interpreted model IV requires an unrealistic supply of colonizing forms, and hence it is likely that successful colonists have adapted to island conditions. However, if local maxima in the density landscape are effective in constraining and channelling morphological evolution, then the potential influence of coevolution is diminished. This is because two species morphologically different enough to coexist would probably evolve to exploit different local maxima: divergence would occur, but it would not be driven by competition. This does not mean that coevolution is unimportant in the finches, since local maxima in polymodal landscapes may not all be effective in constraining morphology. In this situation, and on islands like Fernandina where only one density maximum was detected (fig. 4), coevolution may explain the origin and/or maintenance of large morphological differences between species.

The procedures used in this study are conditional upon observed seed characteristics of islands, but they do not preclude possible interactions between finches and seeds. For example finches influence overall seed density seasonally and annually through consumption. Interestingly this does not seem to have a major influence on the results, as indicated by analyses of some islands in late wet season, following the major burst of seed production; in the late dry season, by which time seed abundance has been greatly depleted; and in different years. This robustness is again due to gaps in the frequency distribution of seed size-hardness classes (e.g., table 1). Few such classes are present on any island, and their presence/absence largely determines the position of local density maxima. This has a more profound influence on predicted morphological patterns than does variation in seed density, which usually influences only the heights of local maxima. However, if finches commonly influence the occurrence of seed size-hardness classes, then seed consumption may be worth considering in an expanded community model.

Coevolution between seeds and finches is another factor which might be considered. Feeding efficiency of a given finch species on seeds tends to increase with seed size within the preferred range, but drops steeply near the upper hardness limit (Schluter 1982*b*). Seed predation therefore may exert a strong selective pressure on some seeds to become harder, favoring in turn a larger finch. A possible example is the *Opuntia* seed on Champion (and nearby Floreana). This is the hardest seed produced by the genus *Opuntia* in the archipelago, and is responsible for the tall peak corresponding to a very deep beak on this island (fig. 4). *Geospiza magnirostris* consumes *Opuntia* seeds on many islands where this seed is present, and the Champion-Floreana *G. magnirostris* was, before its extinction, the largest form of this species in the Galápagos (Lack 1947).

This study was based on analysis of generalist granivores in *Geospiza*, but its basic conclusions are not altered when the other major seed consumers are considered. For example the cactus finch, *G. scandens*, is a major seed consumer in the dry season on only a few islands, but on these it takes some seeds consumed also by *G. fortis* (e.g., Daphne; Smith et al. 1978; Grant and Grant 1980*a*). Removing from consideration the most important seed common to their diets on this island (*Opuntia*) does not alter the basic form of the density curve (fig. 4), though the size of the largest maximum is reduced. Such removal is an unnecessarily drastic way to accommodate the presence of *G. scandens*, since this species also shows important microhabitat differences from the generalist granivores (see earlier). In like manner, the presence of doves and native rats on some islands can be accommodated by the procedure.

Indeed, the procedure used here could in principle be expanded to include these other species, and the rest of the Darwin's finches. This would entail use of a greater number of morphological dimensions to characterize use of resources, and a more complex set of functions relating morphological distance to ecological differences. It is expected that many of the conclusions drawn from the granivorous finches would apply to this larger group. Darwin's finches are strikingly different in their habits (Lack 1947; Grant 1981*b*) and this may reflect the general importance of competitive refugia (model IV) in determining coexistence. Polymodality may also be a general phenomenon: many of the diet differences are qualitative (e.g., herbivory vs. insectivory), and there are likely to be important fitness trade-offs involved in specializing in one mode versus the other.

Finally, these procedures might be used to predict morphological patterns in mainland communities. Again it is unlikely that one morphological dimension will suffice to summarize resource use of species, particularly when complicated microhabitat specializations are involved. An interesting problem for future empirical investigation is whether curves describing population fitness as a function of morphology are also polymodal in these situations. Polymodality is not a requirement for prediction of morphological patterns, but it may render predictions more robust under alternative initial assumptions. In any event, there is no doubt that research into morphological patterns and community structure will profit from attention to details of resource abundance, distribution, and use.

SUMMARY

A procedure is developed and applied to evaluate alternative explanations for morphological patterns in communities of Darwin's ground finches. The first step in the procedure is the computation of expected population density for a hypothetical solitary finch species on an island, as a function of beak depth. This was done for 15 Galápagos islands where food characteristics have been measured. The second step involves construction of hypothetical finch communities for these islands using five different models. Models differ in the extent to which processes

of assembly and/or evolution favor species of high expected density, and in the extent to which interspecific competition influences these processes. By comparing predictions of models to actual communities, the roles of food supply and competition could be assessed.

Results reveal that expected density is usually a polymodal function of beak depth. Islands differ substantially in the shapes of their density functions. Mean beak sizes of species actually present on each island correspond to local maxima in expected density. However, two species never occupy the same or closely adjacent local maxima. Simple models incorporating the effects of both food supply and interspecific competition on assembly/evolution are shown to accurately predict observed morphological patterns. The results support the hypothesis that both food supply and interspecific competition have determined morphological properties in communities of these finches.

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APPENDIX

GALAPAGOS ISLANDS STUDIED, AND THEIR GROUND FINCH SPECIES

Islands	No. Sites	Month Studied	No. *Geospiza* Species	Generalist Granivores	Other Populations
Pinta	6	November	5	*fuliginosa* *fortis* *magnirostris*	*difficilis* *scandens*
San Salvador	2	September	5	*fuliginosa* *fortis* *magnirostris*	*difficilis* *scandens*
Fernandina	4	October	4	*fuliginosa* *fortis* *magnirostris*	*difficilis*
Rábida	1	June	4	*fuliginosa* *fortis* *magnirostris*	*scandens*
Marchena	2	October	4	*fuliginosa* *fortis* *magnirostris*	*scandens*
Genovesa	3	September	3	*difficilis* *magnirostris*	*conirostris*
Santa Fe	1	January	3	*fuliginosa* *fortis*	*scandens*
Plazas	1	March	3	*fuliginosa* *fortis*	*scandens*

Champion	1	January	3	*fortis* *magnirostris*	*scandens*
Española	3	October	2	*fuliginosa* *conirostris*	
Gardner (near Esp.)	3	May	2	*fuliginosa* *conirostris*	
Wolf	1	September	2	*difficilis* *magnirostris*	
Daphne	1	January	2	*fortis*	*scandens*
Tortuga	1	November	1	*fuliginosa*	
Los Hermanos	1	April	1	*fuliginosa*	

NOTE.—*Geospiza magnirostris* is inferred to have been present on Champion and then to have become extinct; this happened as a result of human settlement on nearby Santa María (Lack 1947; Sulloway 1982). Food supply information from most islands was collected by the first author (Schluter 1982*a*, 1982*b*; Schluter and Grant 1982, MS, unpubl.). Additional data were obtained from Abbott et al. (1977) for Rábida, Plazas, and Gardner; from Smith et al. (1978) for Santa Fe; and from T. D. Price (unpubl.) for Daphne and Champion. Sampling methods were identical in each case. The number of sites was determined by time constraints and the diversity of habitats present. One island, Santa Cruz (Smith et al. 1978), was excluded from consideration because data are available for only a small number of habitats.

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