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WORLDWIDE LIMITATION OF FINCH DENSITIES BY FOOD AND OTHER FACTORS[1]

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Abstract. We compared nonbreeding finch densities (biomass) with seed abundance in arid and semiarid sites in Kenya, the United States, Brazil, and Argentina. Our objectives were to examine whether densities are limited by food, and whether a given seed abundance results in similar finch densities on different continents. We also wished to estimate the relative roles of food and other biotic factors in determining absolute density, by comparing the observed densities to those that might potentially be achieved on a given food supply. We used data from the finches of the Galápagos Islands as an approximate measure of the food-imposed upper limit to finch density because food there is short, emigration is restricted, and predation is reduced.

Half the variation in finch densities across sites around the world could be explained by standing seed abundance, strongly suggesting that finches on mainlands are food limited. Densities on different continents were roughly similar when seed supplies were the same, despite the different phylogenetic origins of finches present. Nevertheless, average densities on mainlands were only about one-quarter the densities found on Galápagos islands. Low mainland densities possibly result from competition with other granivores (e.g., rodents and ants). However, mainland finches restrict their foraging to areas of relative safety, where seed densities may be lower than elsewhere, hinting that predation may also reduce densities. We suggest that predation and possibly other biotic factors limit mainland populations jointly with food, and do not simply reduce densities below a point where food is limiting.

Key words: Argentina; Brazil; finch communities; finches; food limitation; limitation by predation; population limitation; seed abundance.

INTRODUCTION

The sizes of many animal populations are limited by food. This is especially true of birds, whose densities are frequently seen to track food supplies (Lack 1954, Pulliam and Parker 1979, Newton 1980, Jansson et al. 1981, Schluter 1982, Grant 1986*a*, *b*, Sinclair 1989, Wiens 1989). The impact on population size of other biotic variables such as predation, disease, and emigration is more uncertain (Sinclair 1989, Wiens 1989), and the relative contributions of food and these other factors in determining absolute density are essentially unknown.

If food is limiting, then more of it results in higher consumer density (this is our definition of food limitation; cf. Wiens 1989). Therefore, a straightforward test of food limitation is the comparison of population density with food abundance across independent sites or time periods. Four general results are conceivable a priori (Fig. 1), and each suggests a different role for food and other biotic factors in determining absolute density. In the first (A), density is unrelated to food abundance; other factors keep populations well below the food-imposed ceiling independently of food supply. A second possibility (B) is that densities range freely between near-zero and the ceiling. Food is limiting overall, in that more food yields more animals on average, but its role is merely to set an upper bound to population size, which for the most part is determined by other factors. The distinct feature of this relationship is a lower limit to population density that is unrelated to food abundance.

A third pattern (Fig. 1C) results when food is all important. Density is strongly associated with food abundance and fluctuates around the food-imposed ceiling; other factors have little impact. Finally (D), food may limit density jointly with other biotic variables, as evidenced by subceiling densities that nevertheless increase steadily with increasing food supply. This latter situation is not implausible; in theory, food can limit populations even in the face of a substantial reduction of total numbers by predators (McNamara and Houston 1987). These four patterns are qualitative and illustrate the most distinct possibilities. In reality intermediate relationships are conceivable.

In this paper we compare nonbreeding density of finches with standing seed supply across localities on three continents. Our purposes in carrying out the study were threefold. First, we wished to test whether finch densities in mainland sites are generally predictable

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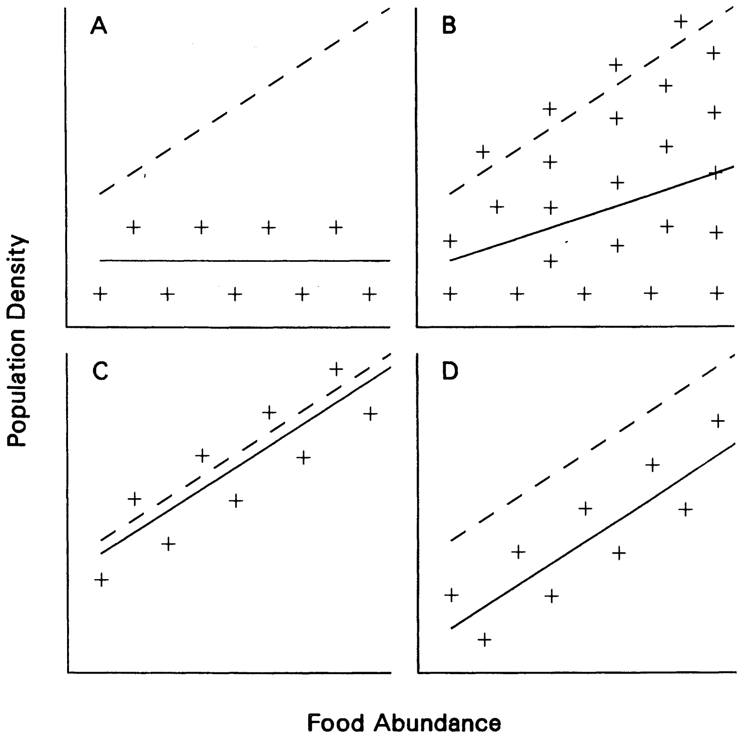

FIG. 1. Hypothetical relationships between population density and food supply (solid line) across independent sites or time periods (+). Dashed line represents the ceiling density imposed by food. The four cases represent four possible roles for food and other factors: (A) limitation entirely by other factors; (B) food constrains only maximum density; (C) limitation entirely by food; (D) strong joint limitation by both food and other factors.

from food supplies, as has been noted previously in specific cases (Pulliam and Parker 1979, Capurro and Bucher 1983, Schluter 1988*a*). An association between finch density and food abundance across such widely scattered locations would provide as strong a test of general food limitation as could be gained from purely comparative study. Second, we wished to determine whether a given seed abundance results in similar bird densities on different continents, despite the different phylogenetic origins of finches present.

Finally, we wished to see whether finch densities on mainlands approach those previously reported for ground finches on the Galápagos Islands. The comparison with Galápagos was of interest because the densities there are likely to be near maximal for a given food abundance. Our evidence is that the sizes of ground finch populations fluctuate seasonally and annually in unison with seed abundance, and standing seed supply in the nonbreeding season on any island accurately predicts the density of finches (Smith et al. 1978, Grant and Grant 1980, Schluter and Grant 1984*a*, Grant 1986*a*, *b*). Additionally, predation rates on adult and nestling finches are lower on Galápagos islands than on mainlands, and emigration of individuals is restricted by the ocean boundary. Therefore, in representing an approximate ceiling, the Galápagos densities allowed us to make a first estimate of the role of food and other factors in limiting finch numbers on mainlands (cf. Fig. 1).

METHODS

Study sites

Study was carried out in the nonbreeding season because the finches are mainly granivorous at this time, and seed abundance is easily quantified. Also, previous studies of Galápagos finches showed that densities are most strongly related to food supply in the nonbreeding season (see *Introduction*). Mainland studies were carried out in Kenya, Brazil, Argentina, and California. Locations in Kenya and Brazil were broadly comparable to Galápagos and to one another in regimes of temperature, precipitation, and vegetation structure, and data are equivalently from the dry season. Fieldwork in Argentina and California was carried out in winter, in convergent warm desert habitats (Orians and Solbrig 1977).

The Kenya study took place between June and October of 1985 and 1986. Habitats were mainly semiarid, and included woodland, wooded grassland, and thorn scrub (Schluter 1988*a*). Four months were spent at one location, Olorgesailie, while visits to five other locations lasted ≈3 wk each. Two field sites were studied at most locations, except Olorgesailie where five sites were used, and a coastal woodland location where only one site was established. Sites within a location were <1 km apart, while locations were separated by at least 50 km.

Brazil was visited between July and September of 1987. Study was carried out near Floresta and Orocó, two locations ≈100 km apart in the semiarid region of southern Pernambuco province. Two sites were established within each location, and were separated by <1 km. The habitat consisted of a mixture of "caatinga" (thorn scrub) and wooded grassland (e.g., Mares 1985). One month was spent at each of the two locations.

Work in Argentina was carried out between July and September of 1987 at Bolsón de Pipanaco in Catamarca province (Orians and Solbrig 1977). A field site was established in each of four habitat types: creosote flat, alluvial fan, thorn scrub, and rocky slope. Each site was studied for ≈1 mo. Sites were at least 10 km apart. Work in California was carried out at the Deep Canyon Desert Research Center in the northern Sonoran Desert. Two sites were established in each of three habitats: creosote flats, alluvial fan, and piñon-juniper, described in Weathers (1983). The results presented here are from November and December 1986, when seed supplies reached low levels prior to the period of new seed production in January-February (R. Repasky, *unpublished data*).

Field sites in all areas were 2 ha, and were placed so that the typical vegetation types at a given location would be included. We also attempted to ensure that a range of finch densities was represented, as judged from brief surveys of the habitats immediately upon our arrival to a location. Sites were unsystematically placed in other respects.

Four field researchers each collected data from more than one region, minimizing the problem of multiple observers. These were the authors, D. Schluter (Galápagos and Kenya) and R. Repasky (Argentina and California), plus two long-term assistants, T. Gullison (Kenya and Brazil) and B. Boyle (Kenya, Brazil, and California). Four additional assistants were involved in collecting the present data (two on Galápagos, one in Argentina, and one in California). In all cases we carefully standardized our procedures to minimize variability among observers.

Finches

We defined a finch as any relatively small, mainly granivorous passerine. Faunae in North and South American sites were dominated by the emberizids (buntings, New World sparrows, and Galápagos finches), whereas estrildids (waxbills) and ploceids (weavers and Old World sparrows) predominated in Kenya. Fringillids (true finches) occurred in Kenyan and North American sites. The Fischer's Sparrow Lark (Alaudidae) in Kenya and the Bay-winged Cowbird (Icteridae) in Argentina were included in the study, as they are highly finch like in diet and bill morphology. Species lists are given in Appendix A.

To census finches, an observer walked at a constant pace through the site (250 m/h) counting all finches foraging within a strip 20 m to either side. In a few cases strip width was increased to 30 m in open habitats and reduced to 10 m in dense scrub. The transect line was established using a measuring tape and compass, and was marked with flagging tape to assist in orientation. Surveys took 2 h and were usually carried out between 0700 and 1000 (occasionally 1500–1800). Ten surveys were conducted in each site during a visit. Daily counts were standardized to birds per hour per 10 m to either side of the observer.

Only individuals actively feeding on seeds were counted, in order to exclude birds seen to perch briefly on shrubs or trees while passing through sites. This rule was used in all regions, including Galápagos, and so any biases introduced should not affect the comparisons. In the data presented here we have also deleted observations of birds consuming nectar or gleaning insects, on the presumption that their immediate presence on the site was not determined by seed density, the only resource being quantified. This decision is conservative: including nongranivorous individuals slightly exaggerates the differences found between mainlands and Galápagos, and does not affect other conclusions.

We were careful to count relatively distant birds (25 m ahead or more) that appeared to flush in response to our approach. We also recorded the perpendicular distance of birds from the transect line as a check on our ability to detect them. Distance was judged visually to the nearest 5 m (i.e., as ≤5, ≤10, etc.) except when birds occurred close to the margin of the census strip (usually 20 m), in which case distance was determined by pacing. We saw no indication from these data that counts declined with distance from the transect line and so we did not correct for it.

Counts were converted to biomass (grams per hour) in order to remove the effects of differences between species in body mass (hereafter, density refers to biomass). This is equivalent to correcting the numerical densities for differences between sites in the body masses of finches present. An alternative metabolic-based correction using body mass$^{0.75}$ was also tried, but the results were unchanged.

Social behavior of feeding finches in the nonbreeding season was relatively similar in all areas. A few Kenyan species defended group territories (e.g., the Grey-capped Social Weaver, *Pseudonigrita arnaudi*), but individuals of most species moved about singly or in flocks. This range of behaviors, from solitary foraging to flocking, was exhibited also by the small Galápagos finches (Schluter 1984).

Diets

Diets of continental finches were determined using an emetic administered to birds captured in mist nets (Schluter 1988*a*). A picture of the total diet of each

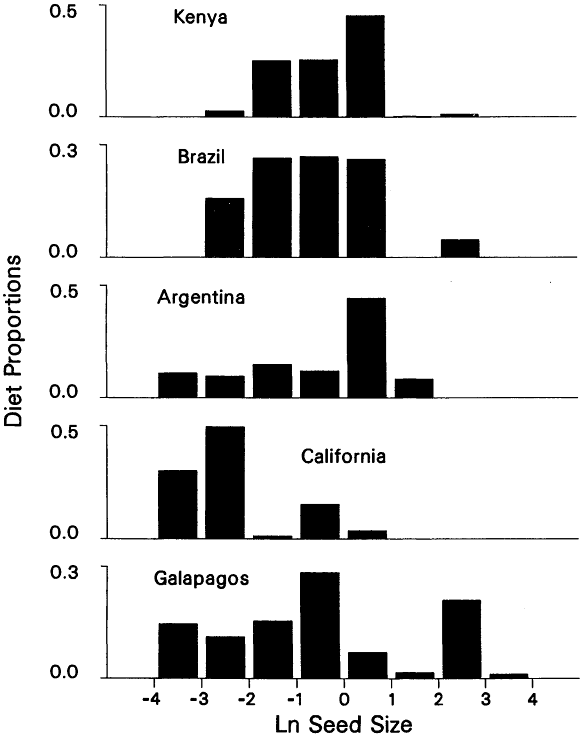

FIG. 2. Composite diet of finches present in each continental region, and of the small ground finches on Galápagos islands. Proportions are averages over member populations or species weighted by population density. Original units are seed mass (mg).

finch community was then obtained by averaging the diet proportions of individual species weighted by density (Fig. 2). Composite diets in all areas consisted mainly of seeds of mass between 0.05 and 2.70 mg (−3 to +1 on the ln scale). Finches in California and Argentina additionally took smaller seeds; some larger seeds were also consumed, especially in Argentina and Brazil (Fig. 2).

One finch present in the piñon-juniper site in California, the Rufous-sided Towhee *Pipilo erythrophthalmus,* was found to consume mainly large acorn seeds (R. Repasky and D. Schluter, *unpublished manuscript*). As all the other species in our sites consumed much smaller seeds (Fig. 2), we deleted *Pipilo* from our comparisons.

Food supply

In each mainland study site, 50 1-m^2 quadrats were located using random numbers. Within each quadrat the seeds on the plants were enumerated directly. Ground seeds were counted by collecting surface soil (maximum depth 2 cm) from subquadrats totalling 0.125 m^2 per quadrat, and later sifting through the material on a broad flat tray. Seeds were identified by comparing them to a reference collection of seeds taken from plants.

Seed abundance was estimated as the summed biomass of all edible small seeds, defined as those species found in the diet of at least one finch at any of the locations. Most seeds between 0.05 and 2.70 mg dry mass were judged to be edible by this criterion. However, ripe seeds of certain plant families were consistently ignored by finches (e.g., Malvaceae, Rubiaceae, and Convolvulaceae), and these were excluded. A few apparently edible seeds (e.g., of some grasses) were not consumed by finches in any site at the time of study (Schluter 1988*a*). The phenomenon may reflect real gaps in the finch community diet, or simply measurement error in our estimates of finch species composition and diets. Such seeds were in the minority, and adding them did not change the results.

The taxonomic composition of edible small seeds was similar in different geographic regions, and thus seed abundances in the different regions are broadly comparable. Most plant families were represented on more than one continent (e.g., Commelinaceae, Boraginaceae, Poaceae, and Euphorbiaceae). The grasses (Poaceae) predominated in the diets of finches everywhere, and the genera most abundant on Galápagos were also abundant in continental locations (*Setaria, Panicum, Cenchrus, Bouteloua, Eragrostis,* and *Aristida*).

A notable limitation of these methods is that seed abundance is not identical with seed availability or profitability. For example, we equated seeds on the ground with those found on the vegetation; while finches everywhere exploited seeds from both locations (e.g., Schluter 1988*a*) they needn't have obtained the same rewards when doing so. Similarly, sites differed in the sizes of seeds present, and probably also in the nutritional content and detectability of seeds. However, seed abundance in sites ranged over an order of magnitude, and it is likely that availability was correlated with abundance over this large range. Therefore, seed availability represents an unmeasured source of variation among sites that may contribute to error around all regressions of finch densities on food supply.

Statistical methods

We compared finch biomass to seed supply in different locations using analysis of covariance (ANCOVA). Estimates of finch density (grams per hour) and seed abundance (milligrams per square metre) were first $\ln(x + 1)$ transformed to render homogeneous the error variances around the regressions. Estimates were then averaged over nearby sites (<2 km apart) of the same habitat type and of similar finch species composition in order to ensure independence of observations. For example, all adjacent sites in Kenya were averaged except in two cases (Hell's Gate and Olorgesailie) where nearby sites differed in vegetation and in the dominant finch species present (Appendix A). The result is that even within a continent the individual points in the regressions represent largely different sets of species. The data used in the regressions are provided in Appendix B.

Estimates of food supply and finch density include measurement error, whose effect is to increase the scatter of Y values about the regression line (Snedecor and Cochran 1967). In assessing the role of food, we considered it worthwhile to determine how much of the observed scatter was real and how much was due simply to imprecise measurement. We estimated the underlying variability in finch density for a given seed supply by subtracting from the variance of residuals (MSR) a correction for measurement error: $\mathrm{MSR}_{\mathrm{new}} = \mathrm{MSR} - \epsilon_Y^2 - b^2\epsilon_X^2\sigma_X^2/(\sigma_X^2 - \epsilon_X^2)$. The terms ϵ_X^2 and ϵ_Y^2 are the squared standard errors, pooled across sites, of the individual estimates of food supply (X) and finch density (Y). b is the slope of the regression and σ_X^2 is the uncorrected variance in X. A second effect of measurement error in food supply is to bias downward the estimate of slope (Snedecor and Cochran 1967). We did not correct for this bias because it was slight and because all the regressions were similarly affected.

Galápagos comparison

One goal was to compare finch densities on continents to those found on Galápagos islands, representing approximate ceiling densities for a given food supply. The Galápagos finches include several large-billed finch species that consume larger seeds than do finches on continents (Schluter 1988*a, b*). As a result, we used only granivorous populations of the small ground finches, *Geospiza fuliginosa* and *G. difficilis* (Schluter and Grant 1984*a, b*).

Three Galápagos data sets were available. The first consisted of dry-season densities of *G. fuliginosa* at six sites on Isla Pinta, averages of observations made in August and November 1979 (finch densities and food supplies were similar in these 2 mo). The second set was from the previous May of the same year, corresponding to the early dry season. We assume that these two data sets are independent, because ANCOVA results showed that for a given food supply, residual finch density in a given site in May was uncorrelated with residual density in the same site in August–November ($r = 0.07$, $P > .4$). The third set represented mean finch and seed densities on other islands measured in the middle-to-late part of the dry seasons of 1979 and 1981. All three sets of observations are based on data in Schluter (1982) and Schluter and Grant (1984*a*), but finch density was recomputed to include only birds feeding on seeds when encountered; for reasons given above (*Methods: Finches*).

Methods to estimate finch density and food supply on Galápagos were identical to those used on continents, with one exception. Transect counts of finches were not begun on Pinta before August 1979, and the May densities were estimated instead using mist nets as described in Schluter (1982). Mist net counts (X) were converted to transect counts (Y) using a regression equation derived from measurements of both X and Y in the same sites in August and November ($r = 0.64$, $N = 12$; Schluter 1982). That the May values are estimated differently might be considered good grounds for excluding them. We have kept them in our analyses because they provide a view of Galápagos finch densities early in the dry season when food is relatively abundant. This decision is conservative in that deleting the May values further exaggerates the differences we found between Galápagos and continents.

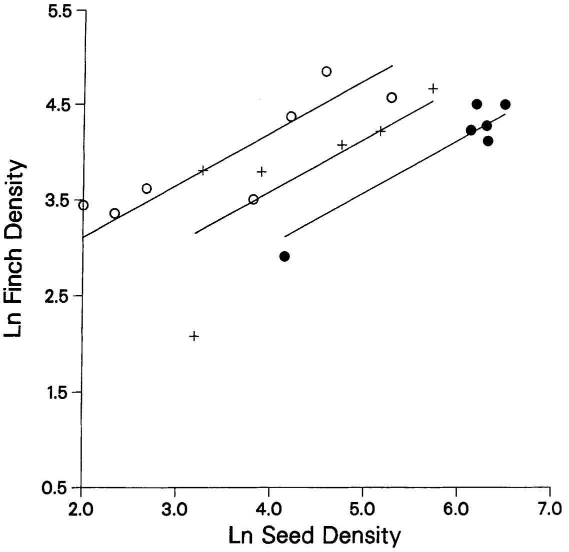

FIG. 3. Density of small finches (g/h), as censused by an observer walking a transect at a steady pace, and small seeds (mg/m^2) in the Galápagos. Regressions for three data sets are pooled to the same slope: sites on Isla Pinta early in the dry season (●); the same sites late in the dry season (+); average densities on Galápagos islands, Pinta excluded (○). Data were transformed using $\ln(x + 1)$.

All seeds consumed by small ground finches were used in the estimates of Galápagos food supplies. They include a slightly broader range of seed sizes than in any of the continental regions (Fig. 2). Several small seeds in the range 0.02–0.05 mg (−4 to −3 on the ln scale) were eaten on Galápagos, as were two relatively large but soft seeds, *Croton* and unripe *Rynchosia* (+2 to +3 on the ln scale).

Galápagos finch densities (Fig. 3) were strongly associated with the supply of small seeds (pooled regression: $F = 33.7$, df = 1,15, $P < .0001$, $R^2 = 0.69$). Slopes were similar among the three data sets ($F = 0.746$, df = 2,13, $P = .49$), but intercepts differed significantly ($F = 7.00$, df = 2,15, $P = .007$). On Pinta, finch density for a given seed supply was lowest in the early dry season, whereas values from the middle-to-late dry season were 1.5–2 times greater. Mean density on other islands was higher on average than in Pinta sites (Fig. 3). Inspection of Fig. 3 raised the possibility that regressions were unduly influenced by two Pinta

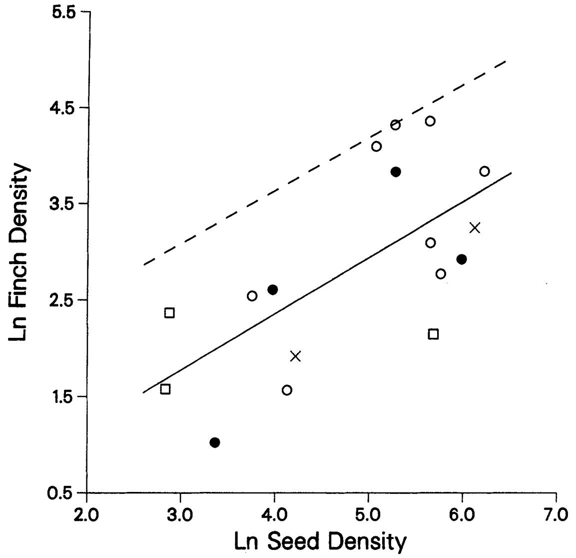

FIG. 4. Density of finches (g/h), as censused by an observer walking a transect at a steady pace, and small seeds (mg/m^2) on continents. Observations are from Kenya (○), Brazil (×), Argentina (●), and California (□). All points, even those from the same region, represent measurements of largely different sets of finch species, and are therefore independent (see Appendices). —— is the regression based on all observations combined. - - - is the pooled Galápagos regression (Fig. 3). All data were transformed using $\ln(x + 1)$.

values (those with $Y < 3.0$), and so we repeated the analysis after deleting them. Results were unchanged (pooled regression: $F = 35.9$, df = 1,13, $P < .0001$, $R^2 = 0.73$; test of equal slopes: $F = 0.165$, df = 2,11, $P = .85$; test of equal intercepts: $F = 4.96$, df = 2,13, $P = .025$).

RESULTS

Nonbreeding finch density on mainlands was positively associated with seed density (Fig. 4; pooled regression: $F = 6.71$, df = 1,13, $P = .022$). Observations from the three continents (Kenya, California, and Brazil–Argentina) overlapped broadly, and regressions did not differ significantly (equal slopes: $F = 1.22$, df = 2,11, $P = .33$; equal intercepts: $F = 0.97$, df = 2,13, $P = .41$). The overall regression, combining points from the three continents, was moderately strong and highly significant ($R^2 = 0.44$, $F = 11.6$, df = 1,15, $P = .004$).

Our estimates of finch density and food supply included measurement (sampling) error, which exaggerates the amount of scatter around the regression line (Fig. 4). We estimated that 30% of the variance of residuals was attributable to measurement error, mainly in finch density. Correcting for this error led to a modified $R^2_{\text{corrected}} = 0.52$. Thus we estimate that approximately half the variation in the density of nonbreeding finches in sites in different parts of the world is explained by seed abundance. Note that this correction does not adjust for variation in food availability above that estimated by food abundance.

Despite evidence of food limitation, densities were low when compared with Galápagos finches over a similar range of seed abundances (Fig. 4). Few of the mainland locations had densities approaching the average Galápagos result, and none matched the highest densities seen on Galápagos islands. Slopes of regressions of finch numbers against food supply were not significantly different among the six data sets (three from Galápagos [Fig. 3] and three from continental regions Kenya, California, and Brazil–Argentina; $F = 0.95$, df = 5,24, $P = .47$), but intercepts were very different ($F = 9.59$, df = 5, 29, $P < .0001$). Mean finch density, adjusted for differences between areas in food supply using ANCOVA, averaged 4.0 in the Galápagos compared with 2.7 on continents (linear contrast [Miller 1981], $F = 37.2$, df = 1, 29, $P < .0001$). On the untransformed scale, this represents nearly a fourfold difference in average finch density between Galápagos (53.0 g/h) and mainlands (13.7 g/h) when seed supplies are the same.

Some of the scatter around the mainland regression may result because our observations constitute a mixture of samples from early to late in the nonbreeding season. This contrasts with the Galápagos regressions, where observations within each line were essentially simultaneous. When compared with the total variance within and among the three Galápagos regressions, which range from early to late in the dry season ($\text{MS}_{\text{residual}}$ + variance among intercepts = 0.51), the mainland residuals were not inordinately variable (uncorrected $\text{MS}_{\text{residual}} = 0.630$). Ideally, the continental residuals could be compared to degree of advancement of the nonbreeding season (e.g., days since last major rainfall), but the necessary data are lacking.

These results allow us to firmly reject the hypothesis that finch density on mainlands is independent of food supply, as depicted in case A of Fig. 1. A significantly lower mean density on mainlands than Galápagos suggests that case C, whereby finch density hovers near a food-imposed ceiling, should also be rejected. Distinguishing between the patterns B and D of Fig. 1 is more difficult, but several lines of evidence suggest that D is the closer representation. First, visual inspection shows that the highest mainland densities were never as high as those observed on Galápagos islands. Eleven of nineteen Galápagos observations fall above the dashed line in Fig. 4 (Fig. 3), whereas not one of the mainland points falls above it. Maximal density on mainlands therefore appears to be lower than would be expected if food alone determined it.

Second, if mainland densities merely take on any value below a ceiling set by food (i.e., case B), then the slope of the mainland regression would be about half the slope of the line representing ceiling density. To test this, we combined the mainland observations into a single data set, and we assumed for simplicity that the slopes of the three Galápagos regressions were equal. We then fit an ANCOVA model to the data, constraining the continental regression to have a slope (β_C) equal to half that of the Galápagos regressions (β_G). A test of the null hypothesis that $\beta_C = \frac{1}{2}\beta_G$ is carried out by comparing the residual mean square of this constrained model to that of a second model in which β_C and β_G are free to differ (Neter and Wasserman 1974). The null hypothesis is rejected at a significance level marginally greater than 0.05 ($F = 4.02$, df = 1,30, $P = .054$). In contrast, an analogous test of the null hypothesis that $\beta_C = \beta_G$ could not be rejected ($F = 0.033$, df = 1,30, $P = .86$).

We also compared the likelihoods of two slopes alternately forced through the mainland data: the pooled Galápagos slope, $\beta_G = 0.551$, and $\frac{1}{2}\beta_G = 0.275$. The first slope ($\beta_G$) was found to be 39.1 times more likely than $\frac{1}{2}\beta_G$. If we consider that β_G and $\frac{1}{2}\beta_G$ are a priori equiprobable, then the posterior probabilities for the two alternative mainland slopes are $P(\beta_G) = 0.975$ and $P(\frac{1}{2}\beta_G) = 0.025$. The mainland data are thus better fit by the Galápagos slope than would be expected under case B.

Third, if case B is correct then the lower limit to finch density should be unrelated to food supply (Fig. 1B). We tested this directly by comparing minimal finch density at low and high food levels using a "smoothed" bootstrap (Efron 1982) having the following steps. First, we computed the mean and variance of finch density at low food levels ($X < 4.5$, $n_1 = 7$; Fig. 4) and then randomly sampled $n_1 = 7$ observations from a normal distribution having the same mean and variance. The mean ($\bar{Y}_1$) and standard deviation (s_1) of this bootstrap sample were used to compute a lower limit, $L_1 = \bar{Y}_1 - 2s_1$. This procedure was repeated for finch densities at high food abundance ($X > 4.5$, $n_2 = 10$) yielding a second lower limit, $L_2 = \bar{Y}_2 - 2s_2$. Finally, we computed the difference between lower limits at low and high food, $d = L_2 - L_1$. This entire sequence was repeated 1000 times, yielding 1000 bootstrap d values. The fraction of d values <0 provides an approximate P value for a test of the null hypothesis that lower limit to finch density does not increase with increasing food. We observed $P = .023$, and therefore conclude that minimum finch density increases with increasing food.

Our results therefore best support case D, whereby density increases with increasing food but is kept below levels that might be achieved if food alone were limiting. Below we discuss possible mechanisms producing this pattern.

Discussion

Demonstration of food limitation

The association between finch density and food supply across widely separated mainland localities strongly suggests that food limits finch density in the nonbreeding season. We interpret this and other results in the following sections. Here we briefly review our procedures and present some cautionary remarks.

Our foremost caveat is that this is a comparative study, not an experimental one, and as a result we cannot conclusively show that greater food levels directly cause greater finch densities. It is always possible that a third, unmeasured factor correlated with food is the actual determinant of density differences. Nevertheless, the comparison of density and food is a valid test of the hypothesis of limitation, and in this case the hypothesis was clearly supported.

A second possible criticism is that finches in all regions are mobile, particularly the gregarious species, and these will tend to congregate in sites having the highest concentration of seeds. As a result, an association between finch density and food supply may merely reflect the capacity of finches to find food, and does not demonstrate food limitation at the population or community level.

However, mobility cannot by itself explain an association between bird density and food supply when study sites are from different habitats or regions, between which birds do not move. To see this, imagine that within each habitat and region birds tend to move into sites of high seed abundance, yielding a linear relationship between finch density and food supply (Fig. 5). If food is not limiting, such that the total number of birds in a region or habitat is unrelated to food, then

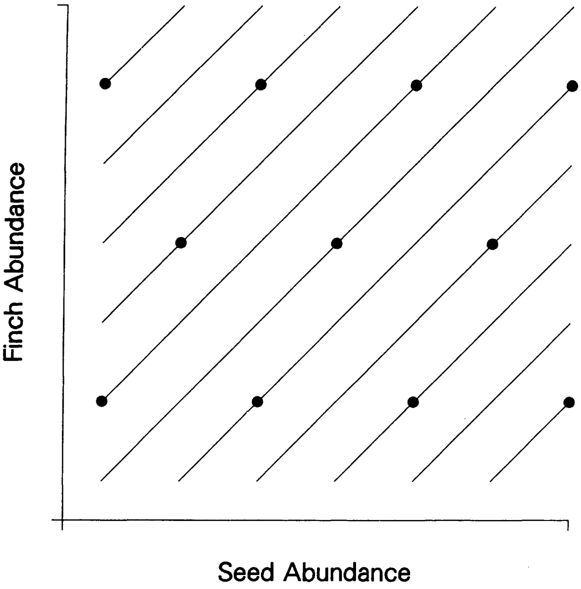

FIG. 5. Pattern expected when individual birds respond to gradients in food density but whole populations are not food limited. Each line represents an independent region or habitat, whose slope reflects the tendency of birds to congregate in local sites of highest seed density. Total finch density is unrelated to food across regions or habitats: lines are parallel rather than superimposed. Symbols indicate measurements in a sample of sites across a range of finch densities, one site per region or habitat.

a sample of sites, one per habitat or region, would reveal little association between bird density and food supply (Fig. 5). A correlation between the densities of birds and food across sites from different habitats and regions therefore implies that the two variables are also correlated across regions and habitats.

Many of our finch species are known to be mobile, and are clearly capable of tracking spatial variation in food supply. A good example is *Quelea quelea,* a highly gregarious African finch that may migrate over large distances while following waves of food production (Ward 1971, Curry-Lindahl 1981). However, within each continent we chose our sites to be as different as possible in habitat so that finch species composition would also be distinct. For example, seeds were relatively abundant at six Kenya locations (Fig. 4) but *Q. quelea* was present at only one, and there was little overlap between the six sites in the most abundant finch species present (Appendix A). Of course, the finches cannot move between regions. As a result, the pattern shown in Fig. 4 provides much stronger evidence of food limitation than would a similar pattern produced from a sample of sites within the same habitat and region.

A third concern is sample size, and the power of resulting tests. Our mainland data comprise 17 points, sufficient to make a preliminary comparison between finches and food but insufficient for more detailed analysis. For example, we failed to detect a difference between regressions from different continents, but we suspect that this is partly a reflection of small sample size. It is tempting to suggest that the true regression for California may be flatter than that for other continents (Fig. 4), and it is equally tempting to postulate an explanation (the California site with highest food abundance is the only continental site that routinely experiences snowfall, which periodically covers most of the available seeds). Elaboration of these and other details await further observations.

Fourth, our comparisons between density and food are complicated by the fact that we have not included all consumers of small seeds. For example, rodents and ants are present on mainlands but absent from the Galápagos, and it is possible that they account for reduced finch densities on mainlands. Doves are another major consumer of small seeds on mainlands, but they are present also on Galápagos in high numbers, and can be considered partly controlled for. Ideally, other taxa could be incorporated into a more complete analysis of granivore density on mainlands and islands, but the data are insufficient at present. Our qualitative impression is that other taxa are probably influential, but that their densities are not generally high enough to make up the nearly fourfold difference in finch density observed between the Galápagos and mainlands. Further quantitative studies are needed.

A final comment concerns the timing of our studies. We cannot rule out the possibility that at some later time in the year, after fieldwork was completed, mainland food supplies did become so reduced that finch densities relative to food abundance approached levels seen on Galápagos. Our mainland studies continued well into the nonbreeding season in most cases and such a critical period, if it exists, must therefore be of short duration. This possibility implies that for most or virtually all of the nonbreeding season mainland densities are determined in large part by factors other than food, the very argument we are attempting to make.

Implications

The association observed between finch density and food supply confirms on a broader scale a pattern seen in more local studies of mainland finches where food supply has been measured (Pulliam and Parker 1979, Capurro and Bucher 1983, Lack 1987, Schluter 1988*a*), and in broad-scale comparisons using climate (rainfall) as a surrogate measure of food abundance (Dunning and Brown 1982). Finch populations appear generally to be food limited.

The roughly similar densities achieved on different continents is notable given the different phylogenetic groups of finches represented—Emberizidae in North and South America, and Ploceidae and Estrildidae in Africa. Previous comparative analyses of finch communities in similar habitats worldwide showed that the sizes and shapes of finch species present are convergent, although some morphological differences associated with phylogeny persist (Schluter 1986). The present study indicates that densities too are similar when food supplies are the same, and suggest that independently evolved finch communities on different continents may be largely equivalent at the fundamental level of bird–seed dynamics.

Food limitation is also an essential precondition for food competition between species, a process hypothesized to have been influential in the evolution of finch communities (Lack 1947, Newton 1967, Schluter and Grant 1984*a*, Grant 1986*b*, Schluter 1988*a, b*). The present results lend support to the view that competition occurs in finches by upholding the key assumption of food limitation. An additional requirement for competition to be present is that finches can significantly deplete seed levels so as to produce effects on later abundances. Such effects have recently been investigated using food-addition experiments carried out in the California desert sites (R. Repasky, *unpublished manuscript*).

Role of other factors

Population studies, especially of birds, often center on the problem of whether food is limiting. Rarely is the additional question posed: Are densities as high as they might be if food alone were limiting? This second problem motivated our comparison of mainland results with the Galápagos finches, where predation and dispersal are reduced and finch densities are likely to be near the maximum density that can be supported by a given amount of food. Our study suggests that finch densities on mainlands are limited by food yet are maintained at only one-quarter of their potential levels. Worded differently, to achieve a particular density of finches requires more food on mainlands than on Galápagos islands. What might account for this difference?

We suggest that factors other than food are partly responsible for low mainland densities but at this point we can only speculate as to what those factors are. We stress that such factors must explain not only the low densities on mainlands, but also the maintenance of food limitation at the reduced densities (Fig. 4). Rather than discuss all the possibilities and their merits we mention one obvious candidate, predation, for which some ancillary data exist (other possibilities include disease and the ease of emigration). Predation is a conspicuous threat in mainland sites but is reduced on Galápagos islands.

A simple way in which predation may affect finch density is to modify the availability of food. For example, predators may exclude foraging birds from areas of high risk and hence from a significant portion of the seed base. In this way population size can be limited both by food (in safe areas) and by predators (in unsafe areas). Evidence from Kenya indicates that predation indeed confines the foraging of finches. Individuals of most species prefer to forage near cover (Fig. 6), and all tend to avoid areas of poor visibility such as under dense vegetation (Schluter 1988*a*; see also Glück 1986, Lima et al. 1987). Fig. 6 suggests that by preferring safer sites birds may forego areas of highest food abundance, as has been observed in other organisms similarly faced with the threat of predation (Sih 1980, Mittelbach 1986, Werner and Hall 1988).

A second possible outcome of elevated predation on mainlands is that birds must spend more time scanning, in effect reducing food availability by reducing feeding rate in all habitats (Pulliam et al. 1982, Glück 1986). The outcome is the same as in the previous example: a greater total density of food would be required to maintain a given density of finches in the presence of predators than in their absence.

Another form of predation that could affect densities is predation on eggs or nestlings. While often dismissed as unimportant (e.g., Lack 1954, 1966), the idea that nest predation lowers population size is frequently suggested by a clear correlation between high adult densities and low nest predation rates (Tomialojc 1978, George 1987). We find that the pattern also holds in finches: reported mean rate of nest failure is higher on average on mainlands than on the Galápagos islands (55 vs. 31%, respectively, based on 35 and 9 studies, $P = .001$), of which nest predation is the main cause (we excluded studies where nesting success was influenced by extreme climate; reference and figures are available from the authors). Of course, the pattern also might result because of a correlation between nest predation rate and the actual causal factor (e.g., predation on adults). As well, the nest predation hypothesis for lower mainland densities encounters a theoretical problem: it is difficult to envision a mechanism whereby population density would be lowered yet food would still be limiting. Nest predation is relatively simple to manipulate, and its true importance may thus eventually be known from experiments.

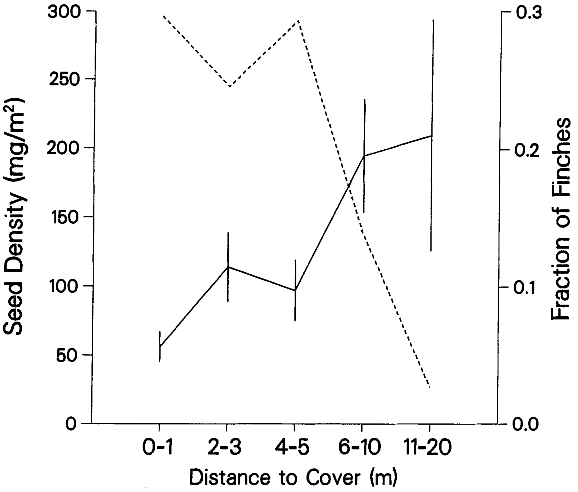

FIG. 6. Seed abundance (——) and finch density (- - -) at Olorgesailie, Kenya, in relation to distance from cover. Cover is defined as any shrub or tree over 2 m in height (Schluter 1988*a*). Finch density was adjusted by the availability of cover: counts in each interval of distance to cover were divided by the frequency of random quadrats recorded in the interval and rescaled to a fraction. Data are from three adjacent sites of similar vegetation, seed density, and finch species, in September 1986 ($N = 1060$ bird observations). Vertical lines are ±1 SE; these could not be computed for finch density.

Studies of natural populations are often carried out on the supposition that if food limitation exists, the role of predation and other biotic factors must be minimal. The finch results hint that this view is too simplistic, and that limitation by both food and other biotic factors (such as predation) may prevail. If the present study is any guide, the effect of these other factors may prove to be quite large.

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APPENDIX A

Density and body mass of finch species at continental locations.* Data were gathered by an observer walking a transect at a steady pace. Species and family names followed Morony et al. (1975).

Finch species	Family†	Density (no./h)	Body mass (g)
Kenya (Bushwhackers)			
Pytilia melba	E	0.85	14.4
Lagonosticta rubricata	E	0.09	9.4
Uraeginthus bengalus	E	0.07	9.6
Ploceus velatus	P	0.17	19.5
Kenya (Shaba)			
Estrilda rhodopyga	E	0.13	7.5
Dinemellia dinemellia	P	0.48	63.8
Plocepasser mahali	P	0.82	37.8
Passer griseus	P	0.19	36.5
Petronia xanthocollis	P	0.06	23.8
Kenya (Athi Plains)			
Serinus atrogularis	F	0.06	10.4
Uraeginthus bengalus	E	0.13	9.6
Uraeginthus ianthinogaster	E	0.04	13.1
Estrilda rhodopyga	E	0.15	7.5
Pseudonigrita arnaudi	P	1.48	19.1
Passer iagoensis	P	0.25	26.2
Sporopipes frontalis	P	0.02	16.8
Ploceus velatus	P	0.11	19.5
Kenya (Hell's Gate 1)			
Uareginthus ianthinogaster	E	0.71	13.1
Passer iagoensis	P	0.09	26.2
Kenya (Hell's Gate 2)			
Emberiza tahapisi	M	0.01	14.6
Serinus atrogularis	F	0.02	10.4
Serinus sulphuratus	F	0.14	23.9
Estrilda astrild	E	0.08	7.7
Passer iagoensis	P	2.51	26.2
Kenya (Sokoke Forest)			
Lonchura bicolor	E	0.49	7.7
Kenya (Olorgesailie 1)			
Serinus donaldsoni	F	0.03	23.9
Uraeginthus cyanocephala	E	0.05	10.0
Estrilda erythronotus	E	0.40	8.5
Lonchura malabarica	E	0.10	9.7
Lonchura griseicapilla	E	0.13	12.5
Pseudonigrita arnaudi	P	0.12	19.1
Passer eminibey	P	0.50	13.4
Petronia xanthocollis	P	0.10	23.8
Ploceus velatus	P	0.03	19.5
Eremopterix leucopareia	A	4.09	14.4
Kenya (Olorgesailie 2)			
Emberiza poliopleura	M	0.01	20.6
Serinus donaldsoni	F	0.01	23.9
Serinus dorsostriatus	F	0.02	14.4
Uraeginthus cyanocephala	E	0.04	10.0
Lonchura malabarica	E	0.03	9.7
Amadina fasciata	E	0.16	15.4
Pseudonigrita arnaudi	P	1.93	19.1
Passer eminibey	P	4.97	13.4
Petronia xanthocollis	P	0.03	23.8
Ploceus velatus	P	0.05	19.5
Quelea quelea	P	0.19	15.3
Eremopterix leucopareia	A	0.10	14.4
Brazil (Floresta)			
Zonotrichia capensis	M	0.05	18.1
Ammodramus humeralis	M	0.19	15.9
Sporophila albogularis	M	0.82	9.7
Coryphospingus pileatus	M	0.73	14.3
Paroaria dominicana	M	0.06	33.2
Passerina (*Cyanocompsa*) *cyanea*	E	0.03	20.7
Brazil (Orocó)			
Coryphospingus pileatus	M	0.36	14.3
Paroaria dominicana	M	0.03	33.2
Passerina (*Cyanocompsa*) *cyanea*	E	0.03	20.7
Argentina (Creosote)			
Zonotrichia capensis	M	0.53	18.0
Diuca diuca	M	0.15	24.1
Poospiza ornata	M	0.05	11.8
Poospiza torquata	M	0.09	10.3
Saltatricula multicolor	M	0.13	22.4
Argentina (Rocky slope)			
Diuca diuca	M	0.05	24.1
Saltatricula multicolor	M	0.07	22.4
Saltator aurantiirostris	M	0.05	42.3
Molothrus badias	I	1.00	41.0
Argentina (Thorn scrub)			
Zonotrichia capensis	M	0.24	18.0
Diuca diuca	M	0.20	24.1
Saltatricula multicolor	M	0.08	22.4
Saltator aurantiirostris	M	0.04	42.3
Argentina (Alluvial fan)			
Zonotrichia capensis	M	0.05	18.0
Saltator aurantiirostris	M	0.02	42.3
California (Alluvial fan)			
Amphispiza bilineata	M	0.31	13.1
Spizella breweri	M	0.02	10.5
California (Piñon-juniper)			
Amphispiza bilineata	M	0.09	13.1
Junco hyemalis	M	0.56	17.3
California (Valley floor)			
Amphispiza belli	M	0.76	15.5
Zonotrichia leucophrys	M	0.03	23.7

* Kenya locations are described in Schluter (1988*a*), California sites in Repasky and Schluter (*unpublished manuscript*). The Rufous-sided Towhee *Pipilo erythrophthalmus* was present in the California piñon-juniper site, but is not included.

† Finch families are Emberizidae (M), Fringillidae (F), Estrildidae (E), Ploceidae (P), Alaudidae (A) and Icteridae (I).

APPENDIX B

Mean density of small seeds (mg/m^2) and finches (g/h) on continents. Data are transformed as ln(x + 1), and are given as means ± 1 SE. Finch species are listed in Appendix A.

Location	Finch density (g/h)	Seed density (mg/m^2)
Kenya		
Bushwhackers	2.78 ± 0.43	5.76 ± 0.14
Shaba	3.85 ± 0.40	6.22 ± 0.14
Athi Plains	3.11 ± 0.48	5.65 ± 0.13
Hell's Gate 1	2.55 ± 0.60	3.75 ± 0.16
Hell's Gate 2	4.10 ± 0.39	5.07 ± 0.11
Sokoke Forest	1.56 ± 0.62	4.13 ± 0.26
Olorgesailie 1	4.37 ± 0.20	5.64 ± 0.14
Olorgesailie 2	4.33 ± 0.16	5.26 ± 0.08
Brazil		
Floresta	3.26 ± 0.19	6.12 ± 0.14
Orocó	1.92 ± 0.23	4.22 ± 0.23
Argentina		
Creosote	2.93 ± 0.30	5.98 ± 0.16
Rocky slope	3.84 ± 0.64	5.27 ± 0.30
Thorn scrub	2.61 ± 0.41	3.97 ± 0.20
Alluvial fan	1.02 ± 0.28	3.36 ± 0.26
California		
Alluvial fan	1.58 ± 0.79	2.84 ± 0.45
Piñon-juniper	2.37 ± 0.34	2.88 ± 0.83
Valley floor	2.15 ± 1.19	5.69 ± 0.33