

THE EVOLUTION OF FINCH COMMUNITIES ON ISLANDS AND CONTINENTS: KENYA VS. GALÁPAGOS¹

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Abstract. I describe the nonbreeding finch community of several habitats in continental Kenya, East Africa, and compare it with previously described communities of granivorous finches on Galápagos islands. The purpose of the comparison is to explore differences in structure between communities that have evolved on a continent and on an isolated archipelago, and to suggest reasons for the differences. The ultimate goal is to infer the factors important in the evolution of finch communities, of which the majority have a continental origin. Four factors that might be expected to influence finch communities differently in Kenya than Galápagos are: a greater diversity of possible competitors, an abundance of predators, movement between localities, and a greater diversity of resources. Differences predicted on the basis of these four factors are compared with actual differences between Kenya and Galápagos, in order to estimate their relative importance.

The communities of Kenya and Galápagos were surprisingly different. Despite the greater age of the Kenya fauna, the diversity of beak sizes was less, the range of seed sizes exploited was less, and the overall utilization of seed resources by finches was incomplete. Species in Kenya were more differentiated by habitat, microhabitat, and seed species, and less differentiated by seed size than finches in Galápagos. Diets were on average more taxonomically specialized, and associations between diet and beak and body dimensions were correspondingly weaker. Kenya finches were sensitive to the proximity of trees and shrubs (cover) while foraging. These results, together with observations from a limited number of other studies, suggest that a dichotomy may exist between the finch communities of continents and isolated archipelagos. However, like Galápagos, local finch density in Kenya was related to food abundance, and diet overlaps between species coexisting in the same locality were low.

Comparison of results with predictions from hypotheses based on the four factors suggests that competition among the large diversity of granivorous species in Kenya (i.e., finches and other granivorous birds, rodents, and ants) is a major reason for the differences between the finch communities of Kenya and Galápagos. The narrow range of beak and seed sizes used by finch species in Kenya is consistent with competition from other taxa, and competition between the many finch species constrained to a narrow range of seed sizes may explain the more pronounced habitat, microhabitat, and diet specializations. Thus, while the finch communities of continents and isolated archipelagos may differ in structure, there is an indication that in large part they represent alternative outcomes of the same process.

Predation risk is the most likely cause of a preference for feeding near cover in Kenya, and it may explain why certain seed resources are not exploited by finches, such as ground seeds in areas of poor visibility (dense grasses). Most species appeared to be similarly sensitive to risk of predation; for example, finch species showed little partitioning along an axis of distance to cover. Thus, the main effect of predation on community evolution in Kenya may have been to further confine the resource spectrum available to finches, a role similar to that of competition from other taxa.

There was no evidence that the effects of competition within localities were swamped by an influx of immigrant individuals and species. However, lesser indirect effects of movement may be present; movement may elevate local species diversity and thereby influence community structure by increasing the diversity of potential competitors and predators. The prediction that a greater diversity of resources in Kenya would lead to a greater diversity of morphological forms was not upheld, suggesting that resource differences are less influential than other factors.

Key words: community evolution; community structure; comparative method; finches; Galápagos; interspecific competition; Kenya; predation.

INTRODUCTION

Ecologists no longer presume that all communities of organisms are structured by the same processes and exhibit only superficial differences associated with tax-

onomy and environment (Strong et al. 1984, Diamond and Case 1986). Instead, appreciation of the variability among communities has revived interest in comparative studies, for example between assemblages that are food-limited vs. space-limited (Roughgarden 1986), comprising vertebrates vs. invertebrates (Schoener 1986a), or situated at different trophic levels (Connell

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1983, Schoener 1983). One goal of comparison is to classify communities on the basis of underlying processes into a small number of types, wherein a subset of general ecological theory might fruitfully be applied (Roughgarden 1983, Schoener 1986*b*). A second goal is to understand the origin and evolution of different community types.

In this paper I describe the nonbreeding finch community of several habitats in continental Kenya, East Africa, and compare its features with those of granivorous finches (*Geospiza*) on the Galápagos Islands. The main purpose of the study is to investigate differences in structure between communities that have evolved independently on continents and on isolated archipelagos, and to suggest reasons for the differences.

Galápagos *Geospiza* communities have been the subject of much recent study (Schluter 1982*a, b*, Schluter and Grant 1982, 1984 *a, b*, Grant 1986), which has shown their structure to be simple and largely determined by two processes: food limitation and interspecific competition for food. Sympatric species of *Geospiza* are strongly differentiated by beak size, and by seed size in the diet, particularly in the dry season when food supplies are low. Finch abundance in the dry season is tied to the standing supply of seeds. A simple model of species presence/absence and coevolution, incorporating available seed supplies and the relation between beak size and diet, predicts the beak sizes of species actually present on islands with a high degree of accuracy (Schluter and Grant 1984*a*).

My interest in comparing *Geospiza* with continental finches stems from uncertainty about the applicability of conclusions from that study to bird communities in general. This uncertainty is founded on two considerations. First, previous studies of finch (sparrow) communities in continental North America by Pulliam (Pulliam and Enders 1971, Pulliam and Mills 1977, Pulliam and Parker 1979, Pulliam 1983, 1985) and Wiens and Rotenberry (Wiens and Rotenberry 1979, 1980, 1981, Rotenberry 1980) have indicated that communities in North America are more complicated and less predictable than those of Galápagos. The comparison with Wiens and Rotenberry is compromised, as their study was conducted in the breeding season when the finches are not mainly granivorous.

Second, it is easy a priori to suggest differences between islands and continents that might cause differences in community evolution. Compared with islands, mainlands may possess

1) *more species of competitors*, including more finch species, plus other avian granivores, rodents, and ants. A consequence for mainland community evolution would be a finer subdivision of resources by finches, and incomplete utilization of available seed resources by the finch component of the larger granivore community.

2) *finch predators*. One possible effect of predation on mainlands is simply to hold finch populations below

the level of food limitation. The consequence for community evolution would be less patterned resource partitioning compared with islands. Or, predation could interact with competition and yield resource partitioning along a risk gradient rather than a simple resource gradient, such as distance to cover (Pulliam and Mills 1977).

3) *movement between geographic areas*, with the possible result that local processes are superseded by regional ones, in contrast to island communities. For example effects of local processes, such as competitive exclusion and character displacement, may be swamped by the movement of individuals and species between localities. A result would be a reduced role of interspecific competition in mainland localities, resulting in less patterned resource partitioning than on islands.

4) *a greater diversity of resources*, and so more avenues for resource partitioning. A consequence would be a greater variety of morphological forms and resources exploited by finches on the mainland than on the island.

Predation and broad-scale movement are particularly interesting, in that each could qualitatively alter the outcome expected on the basis of food limitation and interspecific competition for food. In contrast, differences in resources and the diversity of competitor species involve the same processes on mainlands as on islands, but the outcome in finches depends on these environmental conditions. A comparative study of communities on islands and continents would thus be valuable, as it would yield considerable insight into the forces shaping community structure and evolution.

Continental Kenya was chosen for study for several reasons. Its main advantage is that a variety of habitats and a large diversity of finch species is present in a small geographic area climatically similar to Galápagos. A second reason is that little information was available on the finch communities in Africa, and a study in Kenya would add to the growing body of comparative information on continental finch communities worldwide.

This paper has three parts. In the first, I detail characteristics of the finch community in Kenya, and make comparisons with already published patterns in Galápagos finch communities. Second, similarities and differences observed are corroborated with results from other studies, and used to suggest that consistent differences in structure in fact exist between the finch communities of continents and isolated archipelagos. Third, I compare island–continent differences observed with those expected from hypotheses based on the four factors listed above, in an attempt to estimate their relative importance.

Definitions

I use the term *finch* to refer to all small, seed-eating birds found in the study areas. This includes all granivorous species in the families Emberizidae (bunt-

TABLE 1. Kenya study sites and habitat types. Habitat classification follows Pratt et al. (1966). Mean annual precipitations are from Fenner (1972; Bushwhackers) and Wernstedt (1959; other locations).

Location	Elevation (m)	Annual precipitation (mm)	No. sites	Dates	Habitat
1. Bushwhackers	890	490	2	June 1985	Woodland and bushland (<i>Grewia</i> , <i>Combretum</i> , <i>Commiphora</i> , <i>Acacia</i>)
2. Shaba National Reserve	1020	270	2	July 1985	Bushland and wooded grassland (<i>Grewia</i> , <i>Acacia</i> , <i>Commiphora</i> , <i>Dactyloctenium</i>)
3. Athi Plains	1580	900	2	July 1985	Bushed grassland (<i>Balanites</i> , <i>Themeda</i>)
4. Hell's Gate National Park	1880	600	2	Aug 1985 Sept 1986	Bushland and bushed grassland (<i>Tar-chonanthus</i> , <i>Themeda</i> , <i>Cynodon</i>)
5. Sokoke Forest	15	1030	1	Aug 1985	Woodland (<i>Brachystegia</i>)
6. Olorgesailie Prehistoric Site	1015	370	5	Sept 1985 July–October 1986	Bushed and wooded grassland (<i>Acacia</i> , <i>Dactyloctenium</i> , <i>Aristida</i>)

ings), Fringillidae (true finches), Estrildidae (waxbills), and Ploceidae (weavers). The Fischer's Sparrow Lark (Alaudidae) is also included, as it is highly finchlike in diet and bill morphology.

Most finch species in Kenya are widely distributed, and barriers to movement between study localities are absent; therefore I consider the finches in all Kenya localities combined as constituting a single *community*. The Galápagos finches, on the other hand, though they are distributed over an area of roughly the same size as that spanned by most Kenya sites, live on isolated islands and show interlocality (i.e., interisland) differentiation, and so, consistent with the above use of the term, I refer to the *Geospiza* of each island as a separate community. However, the Galápagos "communities" are not independent from the point of view of comparison with Kenya, and so I describe representative or average features of Galápagos as a whole, and do not compare the Kenya community with each island community separately. Note also that I apply the term community to a taxonomically restricted feeding guild of species. In theory the community refers to all co-existing species, but detailed studies of entire communities are infeasible and in practice the term usually refers to a manageable subset (Roughgarden and Diamond 1986).

METHODS

Field sites

Studies were carried out in 14 sites at six locations, in habitat types along an elevational and moisture gradient from eastern coastal Kenya to the central highlands (Table 1). Locations ranged from humid coastal *Brachystegia* woodland (location 5), to semi-arid bushland and grassland near 1000 m elevation (1, 2, and 6), and moister bushed grassland at 1600–1900 m (3 and 4). Habitat structure was similar to Galápagos in many of the sites, excepting humid coastal forest (Fig. 1).

Mean annual rainfall also varied along the gradient (Table 1), from <300 mm at Shaba, to \approx 1000 mm at the coast and at Athi Plains. This variability in mean rainfall parallels differences between locations in Galápagos, although in the latter case much smaller differences in elevation are involved. For example the southeast coast of Isla Santa Cruz receives \approx 400 mm of rain annually, while a site inland and 200 m higher receives three times that amount (Grant and Boag 1980).

As in Galápagos, rainfall in Kenya is highly seasonal (Fig. 2). Rain in most locations (except the Sokoke Forest) is concentrated into two periods each year, the "short rains" of November and the "long rains" of March to May. Breeding in finches begins with the onset of rain in both periods, and may continue into the beginning of the dry seasons (Brown and Britton 1980). Seed abundance reaches its lowest level in the longer of the two dry seasons, June to October (Lack 1987), and field studies were carried out in this period so as to allow comparison with dry season results from Galápagos. The driest months in the Sokoke Forest are August to March, particularly January–February (Wernstedt 1959). Timing and duration of rains is variable from year to year, but the pattern in the 2 yr of study conformed closely to the average situation (Fig. 2; National Museums of Kenya, *personal communication*).

All six locations were visited in 1985 (Table 1), each for a period of 3 wk. This schedule allowed me to study finches at a variety of locations, but provided only a very short-term view of local patterns. For this reason I adopted a different schedule in 1986, concentrating effort in one of the 1985 locations, Olorgesailie, and repeating observations early (July–August) and late (September–October) in the dry season. One site at Hell's Gate was revisited for a short while between these two stages (Table 1). Four of the six locations (1, 2, 4, and 5) were visited also in 1983, but few quantitative measurements were taken. Two sites were established in 1985 in all locations except the Sokoke

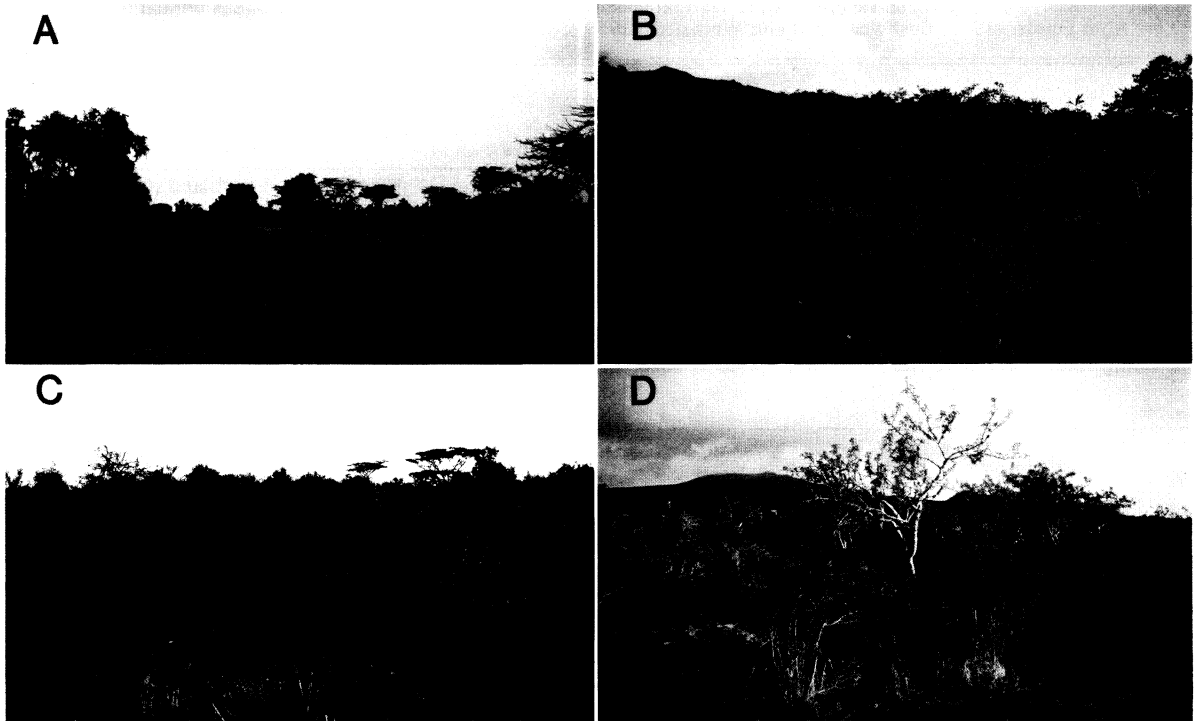


FIG. 1. Comparable sites in Kenya and Galápagos. (A) Athi Plains, Kenya; (B) high elevation site on Isla Pinta, Galápagos; (C) Shaba National Reserve, Kenya; (D) low elevation site on Isla Pinta, Galápagos.

Forest, where one site was used. Three sites were added at Ologesailie in 1986.

Individual study sites were 2 ha, a manageable size for measuring food abundance and total finch density, but relatively small from the point of view of a foraging bird. For example, the same set of species was not always recorded in separate visits to a site (Appendix), mainly because of measurement error. For this reason I usually combined information from all sites in a given location when presenting results. This did not completely solve the problem: a few species thought to use

sites were never formally censused there, and so are not included (e.g., Yellow-rumped Seedeater at Hell's Gate). Nevertheless, the species censused do constitute a majority of those present, and are unlikely to be misleading about community patterns. Diets were obtained for most of these "extra" species from captures around water sources, but none of the results were changed when these data were included. Also, Ologesailie was surveyed more exhaustively than the other locations, but the basic patterns there were found to be no different from anywhere else.

Most locations were in areas of natural vegetation, national parks and reserves, and in one case (Athi Plains) on a game ranch. Of these, Bushwhackers and the Sokoke Forest are somewhat isolated by cleared farms, and no longer experience much herbivory from large mammals. In contrast, four of five sites at Ologesailie are used by Maasai pastoralists to graze livestock, with noticeable effects on the density of many species of grasses and shrubs. It is likely that the finch community has responded to such changes and is now not identical to that prior to the period of heavy grazing.

Finch surveys

Kenya sites were surveyed through transect counts to determine finch abundance, as described for Galápagos in Schluter (1982a). An observer would slowly walk through the site (250 m/h) noting all feeding birds

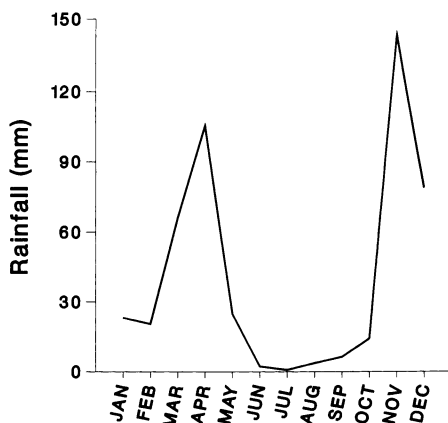


FIG. 2. Mean monthly rainfall at Bushwhackers, Kenya (Fenner 1982).

encountered within a strip 20 m to either side. This was reduced to 10 m in areas of dense vegetation (Bushwhackers) and increased to 30 m in some open sites (Ologesailie). All densities were adjusted to number per hour per 10 m of strip to either side of the observer. We also recorded the perpendicular distance from detected birds to the transect line, to ensure that detection frequency did not fall off with distance. Surveys were 2 h in duration and were done between 0700 and 1000 (occasionally 1500–1800). In most sites, 7–9 surveys were carried out in 1985 and 10 in 1986. Individuals and species obviously not eating seeds during the census were not counted, and thus abundance refers to the number of seed-eating birds.

All analyses of finch communities exclude the rare species, defined as those with average density <0.1 bird/h. This criterion includes species with low density that were seen frequently, but excludes most species that were seen only once in a site. Observations of diet and behavior are available from a few rare species, and their inclusion in analyses did not alter the results.

Finch diets and morphology

We obtained some information on diets through observation of feeding birds. However, data were more difficult to obtain in Kenya than Galápagos, as the birds were more wary of humans and could not be closely approached. I relied instead on stomach contents obtained by using the emetic apomorphine. Finches were captured in mist nets in study sites and at nearby sources of water. Birds were held in the hand while droplets of fresh saturated solution of apomorphine (0.04 g/mL water) were placed in the eyes. Dose was adjusted to body size, ≈ 0.05 mL on average. Birds were held until the droplets were absorbed, and were then placed in a covered container for 15–20 min, the time generally needed for a response. Individuals recovered quickly and flew away when released. No mortality was recorded even among birds captured in the evening and held in bags overnight. Birds were marked with a small notch in the second or third primary, and were often recaptured on subsequent days with no apparent ill effects.

The apomorphine was effective in ≈ 500 of 700 cases, yielding ≈ 180 seeds per individual for 1–45 individuals from each of the 26 finch species (Appendix). We attempted to get samples from at least 10 individuals per species in each visit to a location, though we were not always successful, particularly for the rarer species. However, in a small number of species we were able to make excellent observations of diet during censuses. The number of diet items consumed by individuals was estimated for a maximum period of 300 s, and this information was combined with stomach samples. In the case where birds were foraging in a flock I considered the items eaten by all individuals to constitute only a single sample. Comparison of diets estimated

in this way with diets estimated using stomach contents, in species for which both types of information were available, suggested that the two methods were comparable. None of the results changed when I excluded species whose diets had been estimated in part from observation.

I identified regurgitated seeds either on the same day using a microscope, or later after they were stored in 70% ethanol. Seeds were identified using a reference collection made from plants in study sites and surroundings. Not all seeds could be identified to species (e.g., two species of *Cenchrus* at Ologesailie were difficult to distinguish). In this case, the seeds were grouped at the genus level.

A sample of 10 or more individuals was measured before release. Characters were length of wing, tarsus, and midtoe (in millimetres); beak length, depth, and width (in millimetres); and body mass (in grams). Procedures for most traits are described in Schluter and Grant (1984b) except beak width, which was measured at the anterior end of the nares, and midtoe length, measured from the base of the foot to the base of the nail. All measurements were ln-transformed. Three of the species present in sites were never captured, and I used measurements from museum specimens instead (Schluter 1986). In these cases, mean body mass was estimated from multiple regressions of mass on the six other traits ($R^2 = 0.98$).

Food supply and habitat structure

We estimated seed density in each site as described in Schluter (1982a) for Galápagos. Fifty 1-m² quadrats were located using random numbers, and the number of seeds on the plants within were counted directly. In addition, we collected in bags all surface seeds, litter, and soil (to a depth of 2 cm) in two subquadrats of 0.125 m². I later sifted through the samples on a broad enamel tray and counted all seeds.

We measured vegetation cover in these 1-m² quadrats in 1985. Percent cover of all plant species combined was estimated by eye at ground level (0 m), and in the height intervals 0–0.3, 0.3–0.9, 0.9–1.5, 1.5–3, 3–6, and 6–15 m above ground. When time permitted during finch censuses, we also measured vegetation cover in these same height intervals over the precise location where individual birds were seen foraging.

At Ologesailie in 1986 we measured distance from the 1-m² sampling quadrat to the nearest “cover,” defined as a branch from a shrub or tree at least 2 m tall. Distance to cover was also measured from the location where finches were seen foraging in censuses, so that choice of distance could be compared with availability. The 2 m criterion for cover was based on observation: finches in this habitat did not often flush to shrubs below 2 m in height when we or hawks approached them. This definition of cover is not satisfactory for all species. For example Fischer’s Sparrow Lark re-

mains on the ground or flushes skyward when approached. Nevertheless, 2 m is useful as a basis for initial comparison between species.

Niche measures

I examined diet relationships between finch species using standard measures of breadth and overlap. I used Levins' (1968) breadth index $B = 1/\sum p_i^2$ as it is simple to interpret and has desirable statistical properties (Smith 1982). Measures weighted by food availability were not used because they are less simple to interpret and are more variable. With weighting, breadth in a species that is specialized on exactly one food type fluctuates from site to site, and it is not clear whether this is a result of changing diet or changing food availability. Instead, I computed breadth of seeds available in sites and compared this with diet.

Pianka's (1973) $O = \sum p_i q_i / \sqrt{(\sum p_i^2 \sum q_i^2)}$ was used as a measure of niche overlap, where p_i and q_i are the proportions of food i in the diets of two species. This overlap, like the Morisita-Horn index, has better statistical properties than the commonly used $C = \sum \min(p_i, q_i)$ (cf. Ricklefs and Lau 1980). C also tends to yield lower values of overlap than O on the same data, though both may vary between 0 and 1, and the lower values seemed inappropriate in many of my cases. Finally, with food limitation O is closer to a measure of interspecific, relative to intraspecific, competition than is C , at least under certain conditions (Abrams 1980).

I used seed species as my diet category rather than some grouping of foods by size or taxon. This is potentially dangerous because measures of breadth and overlap are sensitive to the number of food categories, and bias in the estimates increases with this number (Ricklefs and Lau 1980). However, the number of seed species eaten by many finch species was found to be low relative to the number available, and choice of foods was not strongly related to seed size or other natural grouping. Thus, seed species more accurately represented finch diets than any other classification.

All estimates of diet breadth and overlap in Kenya were based on mass of different food types in the diet rather than on the number of items. I used food mass in order to improve comparison with Galápagos, where diets were recorded as the proportion of time spent feeding on different food types; if a finch spends an equal amount of time feeding on a large and a small food type, then it is more likely that an equal mass of food will be obtained from the two than an equal number of items. Mean seed size in the diet was similarly weighted by seed mass. A potential problem remained that Galápagos and Kenya diets were measured in different ways. However, it was possible to convert the Galápagos diets, based on time, to diets based on mass of food using detailed observations of feeding rates (Schluter 1982b). Results were unchanged and for simplicity I present only the unconverted diets.

All measures of breadth and overlap are unfortunately biased, the bias declining with increasing sample size. I wished to determine whether the number of stomach samples from Kenya species was sufficient to compare breadth and overlap with Galápagos results where sample sizes were larger. This was done in two ways. First, I computed rarefaction curves for the estimates (Simberloff 1979) as follows. If breadth was based on N stomach samples then I calculated average breadth also in subsamples of only n stomachs, where n was enlarged in increments from 1 to $N-1$. If overlap was based on N and M stomachs from the two species then I calculated average breadth in subsamples of only n and m stomach, where $n + m$ was increased from 2 to $N + M - 2$, keeping $n/m \approx N/M$. The result is a curve relating average value of the estimate to rarefied sample size (Fig. 3). If the curve asymptotes then sample size is "sufficient"; on average the estimate no longer depends on sample size. If the curve continues to increase then the estimate has not stabilized and bias could be considerable.

Second, I estimated bias using the bootstrap method (Efron 1982, Mueller and Altenberg 1985). If breadth was based on N stomachs then I resampled N stomachs from the data with replacement (i.e., in principle the same stomach could be sampled N times) and calculated breadth. This was repeated 200 times. The difference between the average of these resampled breadths, and breadth in the original data, is an estimate of the bias. Additionally, the standard deviation of these 200 values is an estimate of standard error of breadth. The procedure was the same for overlap except N and M stomachs were resampled from the original N and M stomachs of the two species. Note that in all cases the entire stomach (=sample) is resampled as a unit; to resample the individual items would involve "pseudoreplication" (Hurlbert 1984).

Rarefaction curves for Ologesailie finch diets showed that in most cases mean breadth had reached an asymptote in relation to sample size (Fig. 3A). Exceptions were species with relatively broad diets (e.g., > 3), where the typical sample of ≈ 10 stomachs proved insufficient. Estimates of bias showed that these larger breadths were underestimated by an average of 12%. Mean overlaps were also quite stable (Fig. 3B), with the exception of a few large values in the range 0.4–0.9. Bias estimates suggest that the latter were underestimated by $\approx 9\%$. I did not adjust estimates for bias in my comparisons since few estimates fell within the range affected. The possible effects of bias are discussed when results are summarized.

Standard error of diet breadth averaged 19% of the calculated breadth. The small values of niche breadth recorded for most species (see Results: Diet Specialization) are therefore reasonably accurate in absolute terms. However, large values of breadth (e.g., > 3) should be seen as only rough estimates of the true values. Standard errors for overlaps calculated to lie

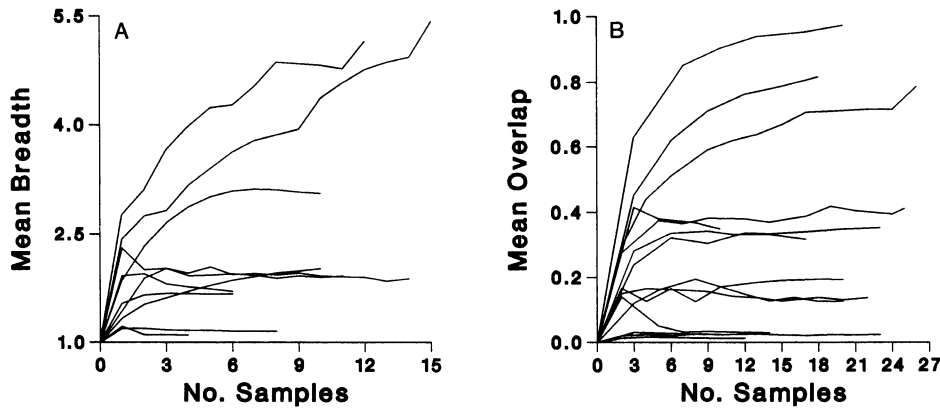


FIG. 3. A selection of rarefaction curves for niche breadth (A) and overlap (B) at Ologesailie, Kenya, July-August, 1986.

between 0.0 and 0.2 averaged 0.0–0.2, large in relative but not absolute terms. Standard errors for higher overlaps ranged between 0.20 and 0.25.

RESULTS

High diversity of finch species

Twenty-six finch species were observed in Kenya study sites (Appendix). This is substantially higher than Galápagos, where only six species of *Geospiza* make up the entire granivorous finch fauna, with no more than five species per island (Lack 1947, Grant 1986). Individual Kenya sites had as many as eight species (Appendix). Six species were present at more than one location (Crimson-rumped Waxbill, Red-cheeked Cordon-bleu, Vitelline Masked Weaver, Rufous Sparrow, Grey-capped Social Weaver, and Yellow-spotted Petronia) but most occurred only once.

The community in Kenya was taxonomically more heterogeneous than in Galápagos, where the finches (Emberizidae) are congeneric. Weavers (Ploceidae) and waxbills (Estrildidae) were the predominant forms, though there were several canaries (*Serinus*, Fringillidae) and one sparrow lark (*Eremopterix*, Alaudidae). High species and taxonomic diversity probably reflects the greater age of the Kenya community compared with Galápagos: many of the Kenya species are the end products of a considerable African radiation (Hall and Moreau 1970), and genera may be up to 10 million yr old (Sibley and Ahlquist 1984). In contrast, *Geospiza* may be as young as 500 000 yr (Yang and Patton 1981).

All of the finch species recorded in Kenya are resident, but one of them, the Red-billed Quelea, may migrate in large numbers over hundreds of kilometres between breeding attempts (Ward 1971, Curry-Lindahl 1981, Jaeger et al. 1986). This species was recorded in study sites at Ologesailie, but only in 1986. Other species may exhibit local movements on a scale of tens of kilometres (Curry-Lindahl 1981). However, the extent of local movements in most finch species is unknown.

Low diversity of beak sizes

Despite the high diversity of finch species in Kenya, range in ln of beak depth measured in millimetres (0.8) was slightly lower than in Galápagos (1.0; Fig. 4). Variance in ln beak depth was considerably lower in Kenya (0.04 vs. 0.11), and the distribution was shifted toward a preponderance of small-beaked forms, of which the majority were waxbills (Estrildidae). Large-billed species were relatively uncommon in Kenya, and none equalled the largest Galápagos finch. Similarly, species with small body mass were more frequent in Kenya, although species with large mass were also present (Fig. 4). Variance in ln body mass was greater in Kenya (0.29) than in Galápagos (0.08).

Incomplete utilization of seed resources

The low diversity of beak sizes in Kenya is associated with a lower diversity of seed sizes in the community diet (Fig. 5). A broad range of seed sizes was present

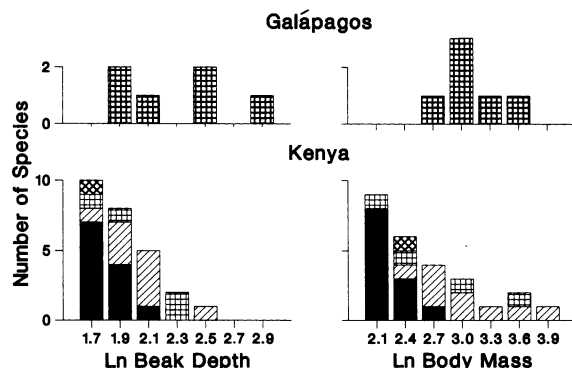


FIG. 4. Histograms of mean beak depth (measured in millimetres) and body mass (measured in milligrams) in the finch species of Kenya and Galápagos. In species that occurred more than once, values are unweighted averages of means from different locations or islands. Kenya symbols refer to families: Estrildidae (■), Ploceidae (▨), Fringillidae (▩), and Alaudidae (▧).

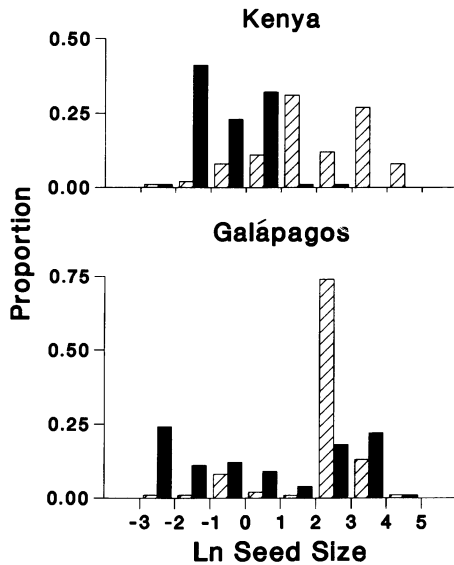


FIG. 5. Use (■) and availability (▨) of seed sizes (measured in milligrams) in Kenya and Galápagos. Diet fractions are based on unweighted averages of all species. Averages weighted by species' abundances gave similar results. Available fraction refers to unweighted averages of all locations. Galápagos results are from Isla Pinta at the end of the dry season 1979 (Schluter 1982a); results from other islands are similar.

in most sites in Kenya, but the largest seeds were not eaten by finches, in contrast to Galápagos. Small seeds were eaten in both places, although seeds of ln mass (measured in milligrams) below -2.0 ($=0.4$ mg) were eaten more frequently in Galápagos than in Kenya. These observations lead to a surprising conclusion: though the Kenya finch community is much older and more speciose, the Galápagos finches have evolved to exploit a greater range of seed sizes.

The relatively small range of seed sizes in the Kenya community diet is not attributable to inedibility of small and large seeds present. Seeds of characteristically unpalatable families (Schluter and Grant 1984a) are not included in Fig. 5, and many of the seeds with ln mass in the range -3 to -2 are grasses. Also, one of the abundant but ignored large seeds in Kenya, *Tribulus*, is present also in Galápagos where it is an important component in the diet of three *Geospiza* species (Grant 1981, Grant and Grant 1982). *Bursera* is another important large seed in the diet of *Geospiza* (Grant et al. 1976, Grant and Grant 1982, Schluter 1982a); large seeds in the related genus *Commiphora* were present but not eaten by finches in most Kenya sites.

The pattern of diets on Galápagos islands is such that all common, nontoxic seed species present in sites are consumed by at least one *Geospiza* species (cf. Schluter 1982a, Schluter and Grant 1984a). However, even within the size range of seeds utilized by Kenya finches, and ignoring the seeds of characteristically unpalatable families, not all seeds were consumed: small

seeds (those with ln mass between -2 and $+1$; Fig. 5) found in study sites but not recorded in the diet of any finch species there constituted on average 30% of the biomass of small seeds available. Even making allowances for species thought to occur in sites but not observed there, a sizable fraction of seeds remain unconsumed by finches. This pattern of incomplete seed use requires further study.

Habitat specialization

Most species of finch are very widespread in East Africa (Hall and Moreau 1970), and their presence in one location and absence from another (Appendix) cannot be attributed to a restricted geographic range. Indeed, species absent from a given location are often present in other habitats nearby. While measurement error may account for a few of the differences among sites in finch species present, habitat specializations of species are also involved. The proximate causes of habitat specialization are varied, in that finches might respond to overall vegetation structure of the area, microhabitat features, or specific food types. It is not my goal to determine which level is the most important in individual cases, I will simply describe specialization in each feature in turn. Here I summarize differences among locations in vegetation structure.

Kenya sites differed conspicuously in vegetation profile. To measure this, I calculated principal components (PCs) from the covariance matrix of vegetation measurements made in 1985, using samples from all available sites combined (Fig. 6A). The variables used were percent cover ($\arcsin\sqrt{p}$ -transformed) of vegetation in seven height intervals (in metres) above ground. The major axes of variation were PC1, density of ground vegetation (0.0 – 0.9 m), mainly grasses, and PC2, density of shrubs and low trees (0.9 – 6 m). These two components together accounted for 64% of the total variation among samples.

Habitat differences among locations are evident from the incomplete overlap of 75% frequency regions (Fig. 6A). The extremes are Bushwhackers, with a high density of shrubs and low trees, Athi Plains, of dense grassland with few shrubs, and Shaba, with its relatively low density of ground vegetation. A third PC axis accounting for an additional 13% of total variance (not shown) further separated locations, distinguishing *Brachystegia* woodland in the Sokoke Forest on the basis of a partial canopy of tall trees (6 – 15 m).

Galápagos *Geospiza* were less responsive than Kenya finches to differences among areas in vegetation structure. Percent cover of vegetation in ground and shrub/low tree layers in samples from five study sites on Isla Pinta were projected onto the Kenya vegetation PCs (Fig. 6B). Samples ranged over as much of the PC1–PC2 plane as in Kenya, although there was greater overlap among some sites. Of the four *Geospiza* species present, three occurred in all five sites and one occurred

in four. A sixth site of dense low humid forest was not included in the comparison as it is very different from all the Kenya sites (Schluter 1982a). Nevertheless, three of the four *Geospiza* species are present there, affirming an absence of strong habitat specialization.

Microhabitat specialization

Measurements of vegetation profile were made in 1985 at the exact spots where individual birds were seen to forage. I calculated principal components from these measurements using observations of all individuals from all species combined. PC1 and PC2 again represented variation in the density of ground vegetation and density of shrubs/low trees, respectively,

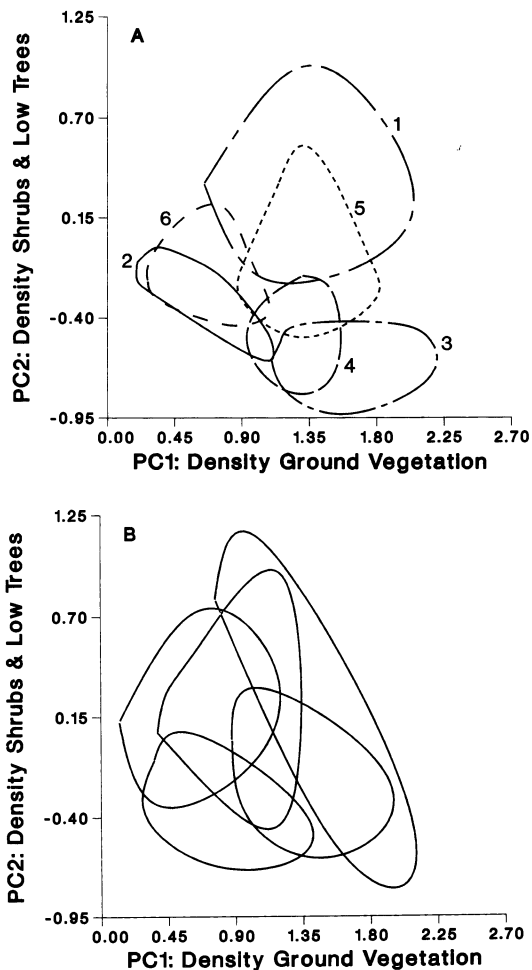


FIG. 6. (A) Vegetation structure in six Kenya locations: (1) Bushwhackers, (2) Shaba, (3) Athi Plains, (4) Hell's Gate, (5) Sokoke Forest, and (6) Ologesailie. Each enclosed region includes $\approx 75\%$ of samples from that location, and was drawn as a smooth curve through octiles of data points around the median. Only two of five Ologesailie sites are included, as vegetation was not measured there in 1986. (B) Vegetation measurements from five Pinta sites projected onto the same axes.

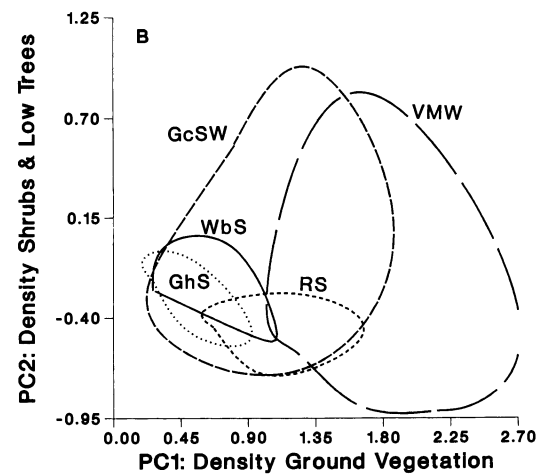
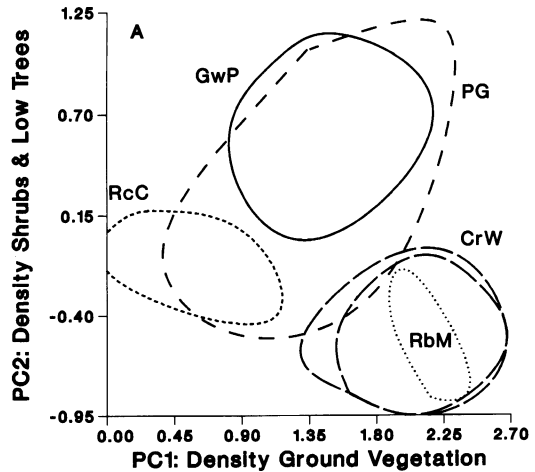


FIG. 7. Vegetation structure at feeding locations used by Kenyan finches, projected onto the same vegetation axes as in Fig. 6. 75% regions were drawn as in Fig. 6. (A) Five species of Waxbill (Estrildidae): Green-winged Pytilia (GwP), Red-cheeked Cordon-bleu (RcC), Purple Grenadier (PG), Crimson-rumped Waxbill (CrW), and Rufous-backed Mannakin (RbM). The two nearly congruent 75% regions for CrW indicate feeding microhabitats at Shaba and Athi Plains separately. (B) Five species of Weaver (Ploceidae): White-browed Sparrow Weaver (WbS), Grey-capped Social Weaver (GcSW), Rufous Sparrow (RS), Grey-headed Sparrow (GhS), and Vitelline Masked Weaver (VMW).

and factor loadings were very similar to those from the previous habitat analysis. For this reason I discarded the PCs derived from finch observations and instead projected the observations onto the habitat principal components (Fig. 7). This projection facilitates the comparison between vegetation structure and study locations (Fig. 6) and their use by finches.

Fig. 7A shows 75% regions for several species of waxbill (Estrildidae) for which at least 25 observations were obtained. Fig. 7B shows the same for several species of weaver (Ploceidae). Three points are illustrated. First, two species present in the same location

TABLE 2. Proportion of seed-feeding observations at different heights, in the Kenyan finch species whose vegetation microsites are shown in Fig. 7.

Species	No. birds	Foraging height (m)		
		0	0-1	1-3
Waxbills (Estrildidae)				
Green-winged Pytilia	28	1.00		
Red-cheeked Cordon-bleu	39	0.87	0.13	
Purple Grenadier	34	0.47	0.50	0.03
Crimson-rumped Waxbill	75		0.91	0.09
Rufous-backed Mannikin	25		0.78	0.22
Weavers (Ploceidae)				
White-browed Sparrow Weaver	42	1.00		
Grey-capped Social Weaver	200	1.00		
Rufous Sparrow	104	0.92	0.08	
Grey-headed Sparrow	20	1.00		
Vitelline Masked Weaver	37	0.19	0.70	0.11

(Fig. 6A) may exploit very different microhabitat types. This was true of the Green-winged Pytilia and the Red-cheeked Cordon-bleu at Bushwhackers (Fig. 7A), and of the latter species and the Crimson-rumped Waxbill at Athi Plains. However, the Grey-headed Sparrow and the White-browed Sparrow Weaver chose very similar feeding microsites at Shaba (Fig. 7B).

Second, species that occupied more than one habitat tended nonetheless to be consistent in their use of microhabitats. The Crimson-rumped Waxbill was common at both Athi Plains and Shaba, which are different in overall vegetation structure (Fig. 6A), but it used a similar microhabitat in each case (Fig. 7A). The Red-cheeked Cordon-bleu also used similar microsites in both the primarily open grassland at Athi Plains and the primarily dense bushland/woodland at Bushwhackers.

Third, species that overlap in microhabitats often do not coexist in the same locations (e.g., Green-winged Pytilia and Purple Grenadier). It is unclear whether such situations reflect unmeasured microhabitat differences among locations, or species responses to other levels of habitat, such as overall vegetation structure or food type.

Differences between species in vegetation profile largely parallel the differential use of perch and ground (Table 2). Species that exploit areas of dense ground vegetation tend to consume food while perched (e.g., Crimson-rumped Waxbill, Rufous-backed Mannikin, and Vitelline Masked Weaver), whereas ground-feeding species prefer areas of reduced ground vegetation (e.g., Red-cheeked Cordon-bleu, White-browed Sparrow Weaver, and Grey-headed Sparrow) (Fig. 7). This pattern reveals an additional way in which seed resources in Kenya were underutilized by finches: ground seeds in areas of dense vegetation were not exploited.

Some microhabitat specialization is found in *Geospiza*, but it is less pronounced than in Kenya. *G. scandens* and one of three populations of *G. conirostris*

prefer areas of *Opuntia* cactus (Grant and Grant 1981). *G. difficilis* takes insects and seeds from litter under areas of dense vegetation on high islands, but it is not so specialized on low islands (Schluter 1982, Schluter and Grant 1982, 1984b). The three most widespread species, *G. fuliginosa*, *G. fortis*, and *G. magnorostris* show little microhabitat preference. All *Geospiza* populations take food from both perch and ground, with the exception of *G. difficilis* on high islands.

Sensitivity to proximity of cover

Virtually all finch species in Kenya fly to nearby shrubs or trees (cover) when approached by human or hawk, and the possibility exists that they are sensitive to the proximity of cover while foraging. This is a special case of microhabitat specialization, but I consider it separately because of its implications for a role of predation in influencing resource use. The main predator of foraging birds is the Gabar Goshawk (*Melierax gabar*), which occurs in most habitats. Other possible predators are the Pale Chanting Goshawk (*M. poliopterus*), the Fiscal Shrikes (*Lanius*), and small mammalian carnivores.

Results from Olorgesailie confirm that most species prefer to feed near cover, defined as a shrub or tree at least 2 m in height (Table 3). Short distances from cover were available more frequently in sites than long distances, but most finch species fed disproportionately often in the 0-5 m range, and few individuals ventured beyond 10 m away. Risk of predation is almost certainly the cause of the pattern. For example, seed density did not decline markedly with distance from cover (Table 3). Most observations were made during the coolest part of the morning, and the pattern was observed on both cloudy and sunny days, ruling out microclimatic explanations. The two exceptions were the Cutthroat, with a modal distance from cover of ≈ 10 m, and the Fischer's Sparrow Lark, which was most abundant in a grassland site having few bushes or trees.

TABLE 3. Frequency of individuals recorded feeding on seeds at various distances from cover in five sites at Olorgesailie, Kenya. "Available" gives the frequency distribution of distances from cover in random 1-m² quadrats (50 per site) and the mean density of small edible seeds in those quadrats.

Species	No.	Distances from cover (m)					
		0-5	5-10	10-15	15-20	20-25	25-30
Grosbeak Canary	6	1.00					
White-bellied Canary	10	1.00					
Blue-capped Cordon-bleu	37	0.95	0.05				
Black-faced Waxbill	12	1.00					
Silverbill	31	0.81	0.09	0.10			
Grey-headed Silverbill	6	1.00					
Cutthroat	189	0.24	0.34	0.32	0.05	0.03	0.03
Grey-capped Social Weaver	908	0.79	0.17	0.04			
Chestnut Sparrow	2781	0.74	0.19	0.06			
Yellow-spotted Petronia	15	0.72	0.17	0.10			
Vitelline Masked Weaver	21	0.71	0.19		0.09		
Red-billed Quelea	165	0.94	0.05	0.02			
Fischer's Sparrow Lark	205	0.13	0.23	0.26	0.21	0.12	0.06
Available							
Distances (fraction)	248	0.62	0.22	0.12	0.03	0.01	0.00
Seed density (g/m ²)							
\bar{X}	250	0.22	0.21	0.31	0.18	0.11	...
(SE)		(0.03)	(0.05)	(0.09)	(0.05)	(0.02)	

The former species usually flew to nearby trees or shrubs when startled, but the latter species did not.

Risk of predation can have interesting consequences for community structure, particularly if it affects competitive interactions. Pulliam and Mills (1977) suggested that grassland sparrows (Emberizidae) in North America may partition seed resources along an axis of distance to cover, in association with differences in predator avoidance strategy. There was little evidence for this in the finches at Olorgesailie: modal distance from cover was 0-3 m for all but two of 13 species.

Preference of most species for cover may be underestimated in Table 3. Most study sites were placed where finches were abundant, and such places tended to include more cover than others. Also, finches selected the taller shrubs and trees: mean height of cover nearest to a foraging finch (3.8 m) was 12 percent higher than mean cover in random quadrats (3.4 m, $t = 2.81$, $n = 297$, 248 , $P = .005$). Availability of sites near preferred cover is thus exaggerated in Table 3.

Quantitative observations of distance to cover were not made in *Geospiza*, but excepting a preference for shade at midday, species did not appear sensitive to cover while foraging. Efficient avian predators are lacking in the Galápagos, although a buzzard (*Buteo galapagoensis*) and the Short-eared Owl (*Asio flammeus*) are present on many islands, and may take finches (cf. Grant 1986).

Weak diet-morphology relations

No strong relationships were observed between diet and beak and body dimensions in the Kenya finch species. This was partly a consequence of the small diversity of morphologies in Kenya compared with

Galápagos, although in the latter cases diet and morphology are usually linked among species as well as among populations and individuals within a species (Grant 1981, Grant and Grant 1982, Schluter and Grant 1984a, b, Price 1987).

For example, all finch species in Kenya consumed seeds of roughly the same (small) size regardless of differences in beak size (Fig. 8). The correlation between beak size and mean seed size in the diet was weak ($r = 0.15$, $n = 21$, $P > .50$), and this was true also when the Estrildidae and Ploceidae were analyzed separately. The correlation is not much improved when heterogeneity in food availability among study locations is considered. For example $r = 0.21$ ($P > .50$) among the 12 finch species at Olorgesailie where at least five samples are available (Grosbeak Canary lacking). The correlation between mean seed size and body mass was slightly higher ($r = 0.36$, $n = 21$, $P \approx .10$). Range in seed size was positively related to beak size ($r = 0.55$, $P \approx .01$), larger-beaked finches taking both smaller and larger seeds than smaller-beaked finches, which tended to specialize on small seeds of intermediate mass (Fig. 8).

A weak relationship between beak size and food size among species does not imply that diet is globally unrelated to beak size. Most seeds consumed by Kenya finches fell within the size range expected from their beak sizes, as judged by regressions of extreme seed sizes in the diet against beak size from among populations of Galápagos *Geospiza* (Fig. 8). Morphology thus certainly constrained diet, but actual diet within the limits set by beak size was primarily determined by other factors.

Microhabitat use was partly related to morphology.

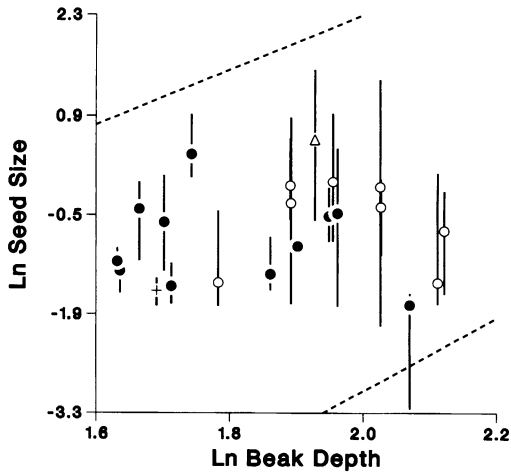


FIG. 8. Beak depth (measured in millimetres) and seed size (measured in milligrams) in the diets of finch species in Kenya. Symbols refer to species means (● Estrildidae; ○ Ploceidae; △ Fringillidae; + Alaudidae). Vertical bars span the largest and smallest seeds that constituted at least 5% of the diet by mass. Dashed lines delimit largest and smallest seeds consumed as a function of beak depth in Galápagos *Geospiza* (after Schluter and Grant 1984a).

I divided the Kenya species into two groups, comprising those that ate seeds most frequently from the ground (>70% of the time), and those that instead ate mainly while perched on stems, twigs, and branches. Overall, there was no significant difference between these two groups when they were compared using all seven morphological dimensions, or using the first two principal components based on the covariance matrix of the seven dimensions (multivariate ANOVA, $P > .40$). Individually only one trait, midtoe length, distinguished the two groups (Fig. 9): regressions of midtoe length against the first principal component based on the seven traits (general size) were of unequal slope (ANCOVA, $F = 14.53$, $df = 1, 20$, $P = .001$). No similar pattern was seen for tarsus length, a trait commonly associated with use of perch (Fretwell 1969, Partridge 1976, Miles and Ricklefs 1984).

Interestingly the regressions in Fig. 9 cross. Small perching species had longer toes than species that fed from the ground, whereas the reverse was true in large finches. The trend held also, albeit more weakly, within the waxbills (Estrildidae), which account for the majority of species feeding from the vegetation ($F = 4.86$, $df = 1, 8$, $P = .058$). The reason for the trend is not clear, but may be related to the different diameter and stability of perches used by small and large finches. The small finches tended to feed while clinging to thin flexible grass stems, while the larger ones used thicker twigs and branches.

Diet specialization

The diets of many finch species in Kenya are relatively specialized. This is partly evident in Fig. 8, where

the range of seed sizes consumed by a given species may be smaller than that permitted by beak size. In addition, finch species had diets composed of a small number of seed species, and this is reflected in relatively low values of diet breadth within locations (Table 4). Several finch species had breadths exceeding 4.0, but most were between 1.0 and 3.0. For example, the Crimson-rumped Waxbill consumed little else but seeds of a single species of grass, *Setaria verticillata*, at both Shaba and Athi Plains, though many other grasses were also present. The diet of the Silverbill at Olorgesailie was composed mainly of seeds of the grasses *Pennisetum mezianum* and *Cenchrus*. The Yellow-spotted Petronia at Olorgesailie ate primarily seeds of the grass *Tetrapogon cenchriformis*.

Diet specializations were sometimes associated with microhabitat specializations. Feeding microsites of the Crimson-rumped Waxbill (Fig. 7A) mainly reflect the vegetation structure of patches of *S. verticillata*, and the finch was present in the two locations having its preferred grass (Appendix). The species was also present at patches of the same grass at Olorgesailie, although not in study sites.

Diversity of seeds in the diet was almost always lower than the diversity of small seeds available (Fig. 10), and the two diversities were uncorrelated ($r = -0.01$). Indeed, the diet breadths of finch assemblages at different Kenya localities show a somewhat similar distribution regardless of food availability (Fig. 10), such that each locality includes both specialized and more generalized species. Using each locality only once (1985 data) I compared mean diet breadths among localities using ANOVA. The resulting F value was < 1 ($F = 0.45$), indicating that the frequency of specialist and generalist species within localities was more balanced than expected (cf. Schluter 1986). The trend was more

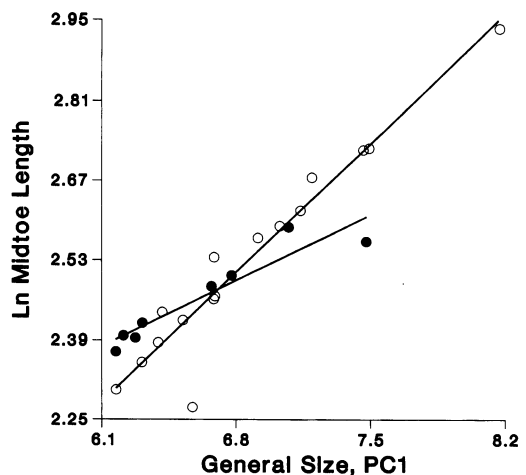


FIG. 9. Regressions of midtoe length (measured in millimetres) against general size in two groups of Kenya finches: those that took seeds mainly from the ground (○), and those that ate seeds while perched on vegetation (●).

TABLE 4. Diet breadth categories (Levin's measure), and the number of seed species constituting at least 5% of the diet by mass, of Kenya finch species. Values are averages across locations and visits. A diet breadth of 1.0 indicates maximum specialization. Only species for which at least five samples were available are presented.

Breadth	Species	Family	No. seed types
1.0-2.0	Green-winged Pytilia	Estrildidae	2.0
	Crimson-rumped Waxbill	Estrildidae	1.5
	Black-faced Waxbill	Estrildidae	2.0
	Rufous-backed Mannikin	Estrildidae	1.0
	Red-billed Quelea	Ploceidae	2.0
	Yellow-spotted Petronia	Ploceidae	2.0
2.0-3.0	Common Waxbill	Estrildidae	3.0
	Purple Grenadier	Estrildidae	3.0
	Blue-capped Cordon-bleu	Estrildidae	3.5
	Cutthroat	Estrildidae	4.0
	Silverbill	Estrildidae	2.7
	Grey-headed Silverbill	Estrildidae	3.0
	White-browed Sparrow Weaver	Ploceidae	3.0
	Fischer's Sparrow Lark	Alaudidae	3.0
3.0-4.0	White-bellied Canary	Fringillidae	4.0
	Red-cheeked Cordon-bleu	Estrildidae	4.0
	Vitelline Masked Weaver	Ploceidae	4.0
	Chestnut Sparrow	Ploceidae	4.0
4.0-5.0	Grey-capped Social Weaver	Ploceidae	4.8
	Rufous Sparrow	Ploceidae	4.0
	Grey-headed Sparrow	Ploceidae	7.0

striking among the three localities with at least four species ($F = 0.12$). The trend was not significant in either case ($P > .20$, two-tailed F tests), but is suggestive.

Diet breadth varied temporally in species with relatively broad diets, but not always in association with absolute food levels (Table 5). The Chestnut Sparrow at Olorgesailie specialized on *Aristida* when this and other seeds were abundant, but had a broader diet at lower food levels. Diet breadth also varied in the Grey-capped Social Weaver, but not consistently with absolute food supply (Table 5).

Diet breadth tended to be higher in the largest species (beak depth: $r = 0.30$, $P > .05$, $n = 21$; body mass: $r = 0.52$, $P < .05$). Breadth was slightly but not significantly higher in the species that fed predominantly from the ground (2.9) rather than the vegetation (2.4; Mann-Whitney U test, $P = .25$).

The Kenya pattern contrasted with that in *Geospiza*, where range of seed sizes eaten for a given beak size was large (dashed lines in Fig. 8). The main consumers of small seeds in Galápagos communities are *Geospiza fuliginosa* and granivorous populations of *G. difficilis*. Breadth of small seeds available to these populations was lower than in many Kenya locations, but diet diversity was usually > 3.0 , and matched or exceeded the diversity of seeds present (Fig. 10). Species specializing on only one or two food types when a variety is available, like the Crimson-rumped Waxbill, are absent. This difference has little to do with differences in the types of seeds available in Kenya and Galápagos. Many of the genera of seeds eaten by finches in Kenya are abundant also on Galápagos islands, including the grasses *Aristida*, *Cenchrus*, *Pennisetum*, and *Setaria*.

The above conclusions are unaffected by the fact that some of the measures of niche breadth in Kenya may be biased downward (see Methods: Niche Measures). Only the larger niche breadths (those above 3.0) are likely to be underestimated, by $\approx 12\%$, but these are relatively infrequent. Results were the same when estimates were corrected for bias.

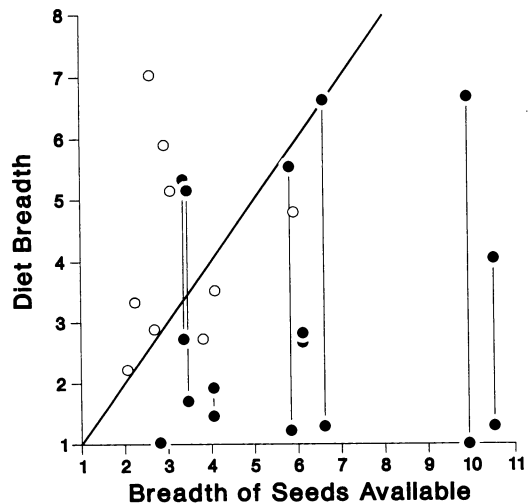


FIG. 10. Diet breadth of Kenya finch species (●) and in nine Galápagos island populations of *Geospiza fuliginosa* and *G. difficilis* (○), in relation to the breadth of seeds available (seed abundances from different sites combined). Available seed breadth uses seeds of ln mass (measured in milligrams) between -3 and $+1$ (cf. Fig. 5). Vertical lines join values for different species from the same location and visit (Olorgesailie was visited three times, Hell's Gate twice).

TABLE 5. Variation in diet breadth and overlap in the Grey-capped Social Weaver (GCSW) and the Chestnut Sparrow (CHSP) in relation to food supply in the three sites where they are most abundant at Ologresailie, Kenya (sites 2–4, cf. Appendix). Only one of the three sites was visited in 1985.

Date	Seed density*	Species	Breadth	<i>Aristida</i> fraction†	Overlap
	(mg/m ²)		\bar{X} (SE)		\bar{X} (SE)
September 1985	133.6 (31.9)	GCSW	3.2 (–‡)	0.01	0.26 (–‡)
		CHSP	4.1 (–)	0.02	
July–August 1986	266.7 (31.7)	GCSW	5.2 (1.0)	0.35	0.79 (0.16)
		CHSP	1.9 (0.4)	0.71	
September–October 1986	117.4 (11.4)	GCSW	6.6 (1.1)	0.05	0.24 (0.09)
		CHSP	4.8 (0.7)	0.24	

* Seed density includes those whose dry mass in milligrams (ln-transformed) is between -2 and $+1$ (cf. Fig. 5).

† *Aristida* fraction refers to the fraction of the diet by mass composed of this abundant grass species.

‡ Standard errors not available for 1985 breadth and overlap.

Low diet overlaps

Diet overlaps between finch species occurring in the same location (habitat) were relatively low (Fig. 11). This is a remarkable result, given that all species consumed seeds of similar size (Fig. 8), and reflects specialization by finch species on different seed types. Eighty-eight percent of recorded overlaps were <0.5 , and 74% were <0.2 . Average (\pm SD) overlap was 0.18 ± 0.26 . Over half (62%) the overlap values were from Ologresailie, where species diversity was highest (Appendix). Average overlap was similar at Ologresailie (0.23) and at other sites (0.11). Results were similar when the larger overlaps were corrected for a slight bias (see Methods: Niche Measures).

Data from Ologresailie, a location visited several times, show that overlaps may fluctuate seasonally and annually in relation to food supply. The pattern is illustrated by overlap between the two most abundant

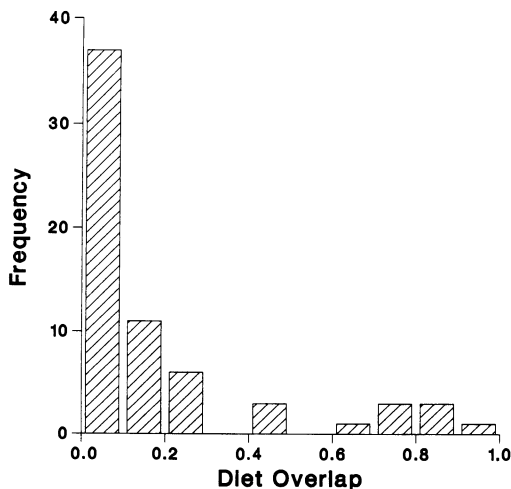


FIG. 11. Frequency distributions of 85 diet overlaps, computed between species in the same locality, separately for each visit. Only species for which at least five diet samples were available are included.

species, and food supply in the three study sites where they predominated (Table 5). Both species consumed *Aristida*, the predominant grass, when food was abundant (July–August 1986), and overlap was consequently high. Consumption of *Aristida* declined at lower food levels later in the 1986 dry season and in 1985, and the diets diverged. A decline in diet overlap with lowered food supplies is commonplace in community studies (Zaret and Rand 1971, Smith et al. 1978, Schluter 1982a, Schoener 1982, Feinsinger et al. 1985), and it is usually interpreted as evidence for competition between species.

Feinsinger et al. (1985) noted a second way in which overlaps could decline with receding food levels: through the departure of mobile opportunistic species. A possible Kenya example is the Red-billed Quelea, which was abundant when food was most abundant, in July–August 1986 (cf. Table 5), and which had high overlap with the Grey-capped Social Weaver (0.82 ± 0.14 SE) and the Chestnut Sparrow (0.97 ± 0.05), a result of its concentrating on *Aristida*. The species was less common in September–October 1986 when food supply was lower, and I did not capture any in mist nets. The species was not present in 1985, when *Aristida* levels were lowest.

Diet overlaps in the Kenya finches are comparable to those between sympatric granivorous species of *Geospiza* (Schluter 1982a, Grant 1986). In the latter case, separation is primarily by food size, although differences in food type are also present as a consequence.

Finch density and food supply

Finch density in sites and visits was correlated with the density of seeds eaten (Fig. 12; $r = 0.73$, $P < .001$, $n = 20$, ln-transformed data). This correlation resulted in part from individual birds preferring to feed in areas of relatively high food density, as evidenced by comparisons among sites within localities (Fig. 12). However, movement does not explain the correlation among locality means ($r = 0.83$, $P < .05$, $n = 6$), since different

finch species are present and abundances are separately determined (Appendix; this is also true to a certain extent among sites within localities). The correlation thus suggests that food levels may limit finch abundance.

I noted earlier that ground seeds in areas of dense ground vegetation (PC1; Figs. 6 and 7) are not exploited by finches in Kenya. This unused resource is reflected in finch numbers in sites: residuals from the regression of finch density on the supply of foods eaten are negatively correlated with the density of ground vegetation (1985 sites only; $r = -0.66$, $P < .05$, $n = 11$). Density may also be related to the availability of cover in sites. In Ologresailie sites in 1986, residuals from a regression of finch numbers on food supply are negatively correlated with the mean distance to cover in sites ($r = -0.67$), and positively correlated with the mean height of the nearest cover ($r = 0.63$). Sample size for this comparison is small, and neither correlation is significant ($n = 8$, $.05 < P < .10$), but the trends are suggestive and in the predicted direction.

Recall that the seed species eaten in sites did not comprise the full set of small seeds available, in part because of measurement error. The correlation between finch numbers and food supply remains significant when all seeds eaten by any species in the locality are included ($r = 0.56$, $P < .05$, $n = 20$). The correlation between finch abundance and the density of all small seeds is weaker ($r = 0.40$, $.05 < P < .10$). A more complete analysis of finch numbers in relation to food supply will be presented elsewhere.

DISCUSSION

The present study compares the structure of communities in similar habitats on a mainland and isolated archipelago. Its approach is similar to that of other "natural experiments" comparing species-rich with species-poor areas (e.g., MacArthur et al. 1972, Cody 1975, Terborgh and Weske 1975, Feinsinger et al. 1985), but it differs from most of these in several respects. One difference is the time scale involved: I have described the outcome of long-term, independent community evolution and adaptive radiation, not simply niche shifts and short-term evolutionary adjustments (see also Cody 1975). Second, my two study areas (Kenya and Galápagos) differ not only in the diversity of competitors, but in other factors that might influence community patterns (see also Feinsinger et al. 1985). Here I summarize the observed differences between island and mainland, and attempt to infer the factors responsible.

Two types of finch communities?

The finch community in Kenya was noticeably different from the *Geospiza* of Galápagos in several interesting ways, summarized in Table 6. An obvious

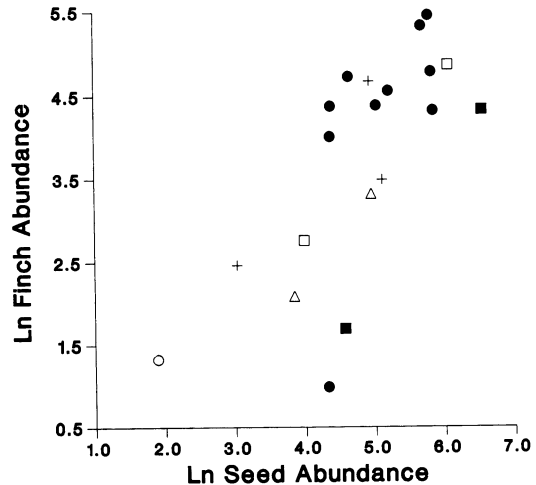


FIG. 12. Total finch abundance and the abundance of consumed seeds (measured in milligrams per square metre) in different sites and visits in Kenya. Study locations are Bushwhackers (△), Shaba (□), Athi Plains (■), Hell's Gate (+), Soko Forest (○), and Ologresailie (●).

question to ask is whether these differences reflect a dichotomy between the outcomes of adaptive radiations in finches on continents and isolated archipelagos, or whether Kenya and Galápagos are merely two of a large number of unique finch communities worldwide. This question can only be answered with a larger number of ecological studies on finches. Such studies are unfortunately few, but the available evidence suggests that consistent island–continent differences do indeed exist.

First, the Hawaiian archipelago is similar to Galápagos, in terms of both its isolation and the amount of in situ evolution that has occurred. The spectacular adaptive radiation of honeycreepers (Fringillidae) there includes a granivorous finch genus, *Psittirostra*, that is similar to *Geospiza* in one important respect: closely related species (i.e., congeners) are highly differentiated by beak size and presumably seed size in the diet (Schluter 1988). Most *Psittirostra* species are now extinct (Olson and James 1982), and little quantitative ecological study has been carried out on the remainder. Comparison of other features of the Hawaiian finches with those of Galápagos and Kenya finches (cf. Table 6) is therefore not yet possible.

Second, independent continental finch assemblages (including Africa) converge in species number and several morphological traits (Schluter 1986), suggesting that many patterns discovered in Kenya apply widely across continents. Finch communities on different continents also usually share the property of a low diversity of beak sizes among the taxonomically heterogeneous species present (Schluter 1988), although this property is not universal (e.g., Newton 1967).

Third, ecological studies of overwintering finches

TABLE 6. Summary of differences between the finch communities of Kenya and Galápagos. Asterisks indicate features that may differ generally between continents and isolated archipelagos.

Features	Galápagos	Kenya	
Entire community			
Diversity of beak sizes	high	low	*
Diversity of seed sizes	high	low	*
Utilization of seed species	complete	incomplete	
Finch species			
Separation by habitat	infrequent	frequent	*
Separation by microhabitat	moderate	frequent	*
Separation by seed species of similar size	infrequent	frequent	*
Separation by seed size	frequent	infrequent	
Diet specialization	low	high	
Morphology-diet relations	strong	weak	
Sensitivity to cover	no	yes	*

(sparrows, Embirizidae) in North America by Pulliam (1985) suggest that, as in Kenya, habitat and microhabitat (but not food size) are primary factors in resource partitioning among species (food species was not compared). However, sympatric continental finches are sometimes differentiated by seed size, in contrast to Kenya: Allaire and Fisher (1975) showed separation of similar-sized sparrows by food species, but also seed size. Newton (1967) described segregation between European finches (Fringillidae) on the basis of habitat, microhabitat, food size, and food species.

Fourth, most finch species on mainlands are probably sensitive to distance from cover. This was demonstrated quantitatively by Pulliam and Mills (1977) and Schneider (1984) for North American sparrows, and by Grubb and Greenwald (1982) for a European weaver (Ploceidae).

It would also be interesting to know whether the differences observed between Kenya and Galápagos are common to other taxa in equivalent situations. Too few comprehensive studies are available to decide this, but some similarities with the present study have been noted in other organisms. For example, the Galápagos and Hawaiian islands include numerous cases of recently evolved plant and animal species distributed across a wider diversity of ecological situations than equivalent species groups on mainlands, where alternative taxa exploit the same niches (Carlquist 1980, Bowman et al. 1983). Diamond (1986) showed that, as in the finches of Kenya, size divergence is uncommon between recent species of New Guinea birds, where avian diversity is high. Williams (1972) argued that size divergence evolves first between West Indies *Anolis* lizard species, with habitat and microhabitat partitioning evolving secondarily on islands of higher lizard diversity. *Anolis* on the West Indies is similar to the Galápagos *Geospiza* in that a number of species have evolved in situ, although the islands are not short of birds and other taxa that might compete with lizards (Wright 1981).

Alternative causes

Why should finch communities evolve such different properties on a continent and an isolated archipelago? Many of the differences observed appear to be consistent with observations of finches from other continents and islands, which would rule out chance and historical quirk as explanations. Instead, explanations should be sought in the processes and conditions that differ between archipelagos and continents. I now turn to an evaluation of alternative factors, using the results from Kenya and Galápagos.

1. *More species of competitors.*—Kenya possesses not only a large number of finch species, but a high diversity of nonfinch granivores. Birds are by far the dominant removers of ripe seeds in Galápagos, and all but one granivorous bird species (the Galápagos Dove, *Zenaidura galapagoensis*) is a *Geospiza*. In contrast, rodents and ants are major seed removers in continental regions, and in combination may predominate over birds (Mares and Rosenzweig 1978, Gillon et al. 1983, Parmenter et al. 1984, Anderson and Ashton 1985). Besides finches, granivorous birds on continents comprise doves, sandgrouse, quail, spurfowl, and francolins, all of which were present in Kenya sites.

With such a diversity of nonfinch seed consumers on continents, it is reasonable to suppose, if food is limiting, that the evolution of finch communities should be partly influenced by competition from them. One influence may be to confine the finch component of the larger granivore community to a particular segment of the available seed spectrum. The observation of a lower diversity of beak and seed sizes in Kenya finches than in Galápagos, despite the greater age of the Kenya finch community, is consistent with the hypothesis of competitive constraints from other taxa. Competition from other taxa may also partly explain the incomplete use of seed species within the narrower size range of seeds eaten by Kenya finches.

Low niche overlaps between finches in Kenya, de-

spite a large number of species confined to a narrow range of seed sizes, also suggests a role for competition between finches. Low overlap was accomplished by a relatively high degree of specialization in habitat, microhabitat and food type. Comparisons between diet and beak and body dimensions in Kenya suggest that in contrast to Galápagos, finch species are more specialized than dictated by external morphology. This pattern of increased specialization in the face of a relatively high species diversity has been noted in several other avian systems (MacArthur et al. 1972, Cody 1975, Terborgh and Weske 1975), and may prove to be a general phenomenon.

2. *Predation.*—Predation on adult finches certainly occurred in Kenya, and it may lower population size. Nest parasitism (Payne 1977) and nest predation also occur in the breeding season. However, there was little evidence from my study that predation prevented food limitation or interspecific competition. Evidence against such a role includes a nontrivial pattern of resource partitioning among species, reductions in diet overlap with reduced seed supplies, and a correlation between the total density of finches and the density of foods they eat in the dry season. Associations between food supply and finch numbers have been noted on other continents where predators are present (Newton 1973, Pulliam and Parker 1979, Capurro and Bucher 1983), suggesting that food limitation generally occurs despite predation.

The clearest evidence of a role for predation in Kenya was the tendency of many species to feed near cover. A second effect may have been to restrict foraging finches to areas of relatively good visibility, to allow detection of predators during an attack (Glück 1986, Lima 1987). For example, most finch species in Kenya took seeds from the ground, but preferred areas of relatively sparse ground vegetation (Fig. 7 and Table 2). This preference is reflected in an inverse relationship between finch abundance in sites and the density of ground vegetation (mainly grasses). Predation risk might thus partly explain the incomplete use of seeds by the Kenya finch community as a whole.

A conspicuous feature of the Kenya community was that predation risk appeared to influence different finch species similarly: modal distance to cover was similar in most *Olorogesailie* species (the main exception was the Fischer's Sparrow Lark), and all species appeared to avoid areas of poor visibility. There was little evidence of resource partitioning along an axis of distance to cover or other risk gradient (Pulliam and Mills 1977). As a result, the major effect of predation on the evolution of finch communities in Kenya may simply have been to confine finches to areas of relative safety, and hence to a narrower segment of the resource spectrum than would otherwise be the case. Rather than eliminating competition between finches, predation in Kenya may restrict the areas where finches compete. In

this role predation risk in finches acts somewhat like competition from other taxa.

Other island–continent differences seem to require an explanation other than simply predation. For example, it is unclear how predation could constrain the overall range of beak and seed sizes in the finch community, but not body masses. Consumption of the smallest seeds might entail great predation risks because they must be consumed at a high rate in order to be profitable, compromising scanning frequency (Glück 1986, Lima 1987). This mechanism would not explain the absence of large-seed consumers: large seeds require husking, and a finch can both scan and husk simultaneously (S. L. Lima, *personal communication*). Most species of large seeds are produced by shrubs and trees, and hence could be eaten in the relative safety of cover.

3. *Movement.*—Galápagos islands are relatively small and isolated from one another by open water, in contrast to continental Kenya, where barriers to movement of individuals across large distances are few (although the actual extent of such movement is not well known). Unlike small islands, the species present in any one continental locality need not constitute a stable assemblage, since local competitive exclusion or character displacement can be greatly slowed or even stopped by recurrent immigration of individuals from elsewhere.

The simple expectation that effects of local processes on mainlands might be swamped by an influx of individuals from elsewhere was not upheld for Kenya, since interesting local patterns were discernible, such as microhabitat specialization, and low diet overlap between coexisting finch species feeding on seeds of similar size. Certain patterns were characteristic of both the study locality and the “region” (the collection of localities) such as the low diversity of beak sizes, the low diversity of seed sizes consumed, and habitat and microhabitat specialization. Most island–continent differences in finch community structure are therefore unlikely to have resulted solely from differences in the amount of large-scale movement.

Movement may nevertheless have indirect consequences for island–continent differences in community structure. A probable role is to elevate the number of species occurring within localities, as suggested for other organisms by a positive relationship between local species diversity and regional diversity, a correlate of the size of the geographic region (Cornell 1985, Ricklefs 1987). This effect may occur in continental finches, as evidenced by consistent differences among mainland regions in the number of species occurring locally (Schluter 1986). The result of such effects is to increase the number of potential competitor (and predator) species, whose direct consequences for differences between the finch communities of Kenya and Galápagos have already been discussed.

4. *Resource diversity*.—The expectation that a greater diversity of resources in Kenya would lead to a greater range of finch morphologies and a greater variety of exploited resources was not upheld. Thus, while differences in resource diversity may exist between Kenya and Galápagos, they appear to be less influential than other factors in causing observed differences in community structure.

A final question to ask is whether the contrasts between finch communities of Kenya and Galápagos are a straightforward reflection of their differences in age. I have not explicitly considered time to be an alternative factor because it cannot by itself be a direct cause of most community differences: finch species are unlikely to evolve along some temporal trajectory (e.g., toward greater specialization) independent of ecological circumstance. Rather, the ecological factors that determine community patterns may change with time. In light of conclusions made above, the most important changes would be in the number of competitor and predator species. For example, were finch species on Galápagos to accumulate in time, greater amounts of habitat and microhabitat specialization might follow, as suggested for *Anolis* by Williams (1972).

Progressively greater resemblance between Galápagos and Kenya is not inevitable for two reasons. First, the diversity of other taxa on the islands will presumably remain low because of isolation. Hence, finches on islands should continue to control indefinitely those resources that are exploited on mainlands by other taxa. Second, movement between localities on mainlands will ensure that a higher diversity of species is maintained than on a smaller island. However, an interesting comparison could be made between Galápagos and Hawaii, since the latter finch communities were older and more speciose (Olson and James 1982) and may have represented a later stage in community development. Such a comparison would help clarify the effects of time on island community patterns.

In conclusion, comparison of finch communities in Kenya and Galápagos permits a tentative answer to the question: what factors are responsible for their differences? Results are consistent with the hypothesis that interspecific competition involving a greater number of finch species and other competitor taxa in Kenya than Galápagos is responsible for most of the differences in community structure. Thus, the appearance of possibly two types of communities characterizing continents and islands may in large part represent alternative outcomes of the same process. Predation in Kenya is also influential, but its main role seems to be to confine finches to relatively safe areas wherein competition for seeds nevertheless occurs. Future comparisons involving other islands and continents would help refine our understanding of the roles of these and other processes, and the extent to which their effects may change with community age.

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APPENDIX

Finch species recorded in site censuses at each of the six locations. Several sites were visited twice: Hell's Gate, site 2 (1985 and 1986), and Ologesailie, sites 1 (1985 and September–October 1986), 3, and 4 (July–August and September–October 1986), and one site was visited three times, Ologesailie, site 2 (July–August and September–October 1986). In such cases, the number of x's indicates the number of visits on which a given species was recorded. Rare species are not listed (see Methods: Finch Surveys). Latin names follow Morony et al. (1975).

Location	Species	Site					
		1	2	3	4	5	
Bushwhackers (2 sites)	Green-winged Pytilia	<i>Pytilia melba</i>	x	x			
	Vitelline Masked Weaver	<i>Ploceus velatus</i>	x				
	Red-cheeked Cordon-bleu	<i>Uraeginthus bengalus</i>	x				
	African Firefinch	<i>Lagonosticta rubricata</i>		x			
Shaba (2 sites)	Crimson-rumped Waxbill	<i>Estrilda rhodopyga</i>		x			
	White-headed Buffalo Weaver	<i>Dinemellia dinemellia</i>	x	x			
	White-browed Sparrow Weaver	<i>Plocepasser mahali</i>		x			
	Grey-headed Sparrow	<i>Passer griseus</i>		x			
Athi Plains (2 sites)	Yellow-spotted Petronia	<i>Petronia xanthocollis</i>	x				
	Red-cheeked Cordon-bleu		x				
	Crimson-rumped Waxbill		x				
	Grey-headed Social Weaver	<i>Pseudonigrita arnaudi</i>	x				
	Rufous Sparrow	<i>Passer iagoensis</i>	x	x			
	Vitelline Masked Weaver		x				
Hell's Gate (2 sites)	Yellow-rumped Seedeater	<i>Serinus atrogularis</i>	x				
	Purple Grenadier	<i>Uraeginthus ianthinogaster</i>	x				
	Rufous Sparrow			xx			
	Brimstone Canary	<i>Serinus sulphuratus</i>		xx			
Sokoke Forest (1 site)	Common Waxbill	<i>Estrilda astrild</i>		x			
	Rufous-backed Mannikin	<i>Lonchura bicolor</i>	x				
Ologesailie (5 sites)	Fischer's Sparrow Lark	<i>Eremopterix leucopareia</i>	xx				xx
	Black-faced Waxbill	<i>Estrilda erythronotos</i>	xx				
	Grey-headed Silverbill	<i>Lonchura griseicapilla</i>	x				
	Cutthroat	<i>Amadina fasciata</i>					x
	Grey-capped Social Weaver		x	xxx	xx		xx
	Chestnut Sparrow	<i>Passer eminibey</i>	x	xxx	xx		xx
	Red-billed Quelea	<i>Quelea quelea</i>		x	xx		x
	White-bellied Canary	<i>Serinus flaviventris</i>		x			
	Grosbeak Canary	<i>S. donaldsoni</i>		x			
	Blue-capped Cordon-bleu	<i>Uraeginthus cyanocephala</i>		x			x
	Silverbill	<i>Lonchura malabarica</i>	x	x			x
Yellow-spotted Petronia		x					
Vitelline Masked Weaver			xx				