Predation, seed size partitioning and the evolution of body size in seed-eating finches

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Summary

I compare the relationship between bill size (depth) and body size among different taxa of seed-eating finches to test the hypothesis (Schluter, 1988a) that in habitats where seed-eating finches are vulnerable to predators, finches have larger bodies relative to their bill size. In support of this hypothesis, ground-foraging finches on continents (Emberizidae, Passeridae, Fringillidae), where predators are more common, have larger bodies relative to their bill sizes than do ground-foraging finches on islands (Emberizidae, Fringillidae). Ground-feeding finches on continents may also be more vulnerable to predators than tree- and shrub-foraging finches. As predicted, in North America, ground-feeding finches (Emberizinae) have larger bodies relative to their bill size than do tree- and shrub-foraging finches (Carduelinae). As a consequence of increased body size relative to bill size, both the range of possible bill sizes and potential seed sizes that can be eaten are reduced. Moreover, increased metabolic demands caused by larger body size may lessen the ability to specialize on a few seed types. These two factors reduce the potential for seed size partitioning. Consequently, vulnerability to predators may limit, and is inversely correlated with, seed size partitioning in seed-eating finch communities. The extent to which predation has influenced other bird communities may be considerable, and the patterns found by Schluter (1988a) and in this study indicate that future ecomorphological studies, especially on species that spend much of the day foraging, might profit by considering predator vulnerability as well as foraging behaviour.

Keywords: Body size, Carduelinae, Drepanidinae, Emberizinae, foraging behaviour, *Geospiza*, Passeridae, predation, resource partitioning.

Introduction

Much recent research has focussed on the manner in which predators influence foraging behaviour (e.g. Caraco *et al.*, 1980; Werner *et al.*, 1983; Brown *et al.*, 1988) and community structure (e.g. Connell, 1975; Shih *et al.*, 1985). Although the effect of predators on social and foraging behaviour of birds has long been recognized (for a review see Pulliam and Millikan, 1982), community level effects on birds are just beginning to be examined (Pulliam and Mills, 1977; Pulliam, 1983, 1985; Schluter, 1988a,b). One obstacle is that predation rates on birds are difficult to measure. Nevertheless, comparisons of communities that differ in risk to predation should prove valuable for evaluating the possible effects of predators on bird communities.

Based on a comparison between seed-eating finch species in Kenya, where predators are common, and finches on the Galápagos, where predators are rare, Schluter (1988a) hypothesized that for a

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given bill size predation may result in selection for larger body size. In support of this hypothesis, body mass increases more rapidly with bill depth among Kenya finches (Fringillidae, Passeridae, Estrildidae) than among Galápagos finches (*Geospiza*; Emberizidae) (Schluter, 1988a).

For large-billed finches, increased body size may improve predator evasion for at least two reasons. First, as body mass increases the proportion of body mass devoted to flight muscles increases because proportionately less of total body mass is devoted to the bill (and, at least among seed-eating finches, skull and associated jaw and neck musculature; Grant, 1986). A larger body mass with proportionately more flight muscles may provide more power for rapid acceleration. Because the power output for flight in relation to body mass scales to a power of less than one (Pennycuick, 1975), larger bodied birds require proportionately greater increases in body mass (flight muscles) for equivalent increases in power. Thus, if power for rapid acceleration is critical for evading predators, then the slope of the curve representing the relationship between body mass and bill depth should increase with increases in vulnerability to predators.

Second, aerodynamic efficiency is improved when the centre of gravity is located between and slightly below the wings, and many characteristics of birds are thought to be adaptations related to weight distribution (Welty, 1975). In particular, the mass of the heads of most birds is reduced, teeth have been lost and the muscular gizzard, which grinds up food, is located near the centre of gravity. A large heavy bill, skull and associated jaw musculature, without counter-balances, reduces aerodynamic efficiency. Hence, increased body mass relative to bill size may improve both acceleration and aerodynamic efficiency and, thus, predator evasion.

The aim of this paper is to (1) determine if there are consistent differences in body size relative to bill size between seed-eating finches that differ in their vulnerability to predators and (2) suggest, given the relationship, how community organization might be affected.

If birds with relatively large bodies, compared to the size of their bill, are better at evading predators (Schluter, 1988a), then those seed-eating finches more vulnerable to predators are predicted to have both proportionately larger bodies and a steeper sloped curve of the relationship between body size and bill size than less vulnerable finches. I make two main comparisons to test this hypothesis. First, I compare two seed-eating finch taxa from North America, the Emberizinae (Emberizidae) and Carduelinae (Fringillidae), that, for two reasons related to their feeding behaviour discussed below, differ in vulnerability to predators. Second, I compare island taxa, which have few predators, to mainland conspecifics or congeners, or other ecologically similar taxa. These island finches should have the smallest body masses relative to bill sizes.

Species

In North America, the subfamilies Carduelinae and Emberizinae are the two major groups of seed-eating birds. Although many species in these two subfamilies rely on seeds (Martin *et al.*, 1951), especially during winter when food may limit population size (Newton, 1972; Pulliam and Parker, 1979; Dunning and Brown, 1982), they differ in ecology in two fundamental ways that should influence the impact of predators. First, carduelines tend to forage in vegetation, often near tree tops (Newton, 1967, 1972; Austin, 1968; Benkman and Pulliam, 1988), whereas emberizines usually forage on or near the ground. Emberizines, therefore, are probably more susceptible to predation than carduelines because the probability of predation is inversely related to the height at which birds forage in the vegetation (Ekman, 1986).

Second, carduelines consume seeds that on average are over one order of magnitude larger than those consumed by emberizines, and can handle large seeds more quickly (Benkman and Pulliam, 1988). As a result, to meet energetic requirements during a winter day carduelines need

to find a seed every 100 to 500 sec, whereas emberizines have to find on average one every 2 to 5 sec (Benkman and Pulliam, 1988; also see Pulliam, 1980, 1985). Carduelines generally locate trees or shrubs with seeds while in flight, rapidly handle relatively large seeds while perched in the tree or shrub, and then fly to a perch, often high in a tree, before continuing to forage or departing in search of another seed patch (personal observation; Benkman and Pulliam, 1988). Consequently, much of the day is spent either flying or perched in relatively safe sites. Emberizines, in contrast, spend most of the day hopping on the ground searching for and handling small cryptic seeds (e.g. Pulliam, 1980). Moreover, because finches cannot scan for predators when securing seeds (e.g. Pulliam *et al.*, 1982), emberizines may be particularly vulnerable to predators when searching for cryptic seeds.

Differences in plumage between emberizines and carduelines provide additional support for the hypothesis that emberizines are more vulnerable to predators than carduelines. Carduelines are much brighter and more conspicuously coloured than emberizines, and because none of the species in either group is known to be commonly polygynous (Verner and Willson, 1969; Newton, 1972), these differences are presumably due to more intense predation pressure on emberizines (Krebs, 1979; Lyon and Montgomerie, 1985).

The rosy finch (*Leucosticte arctoa*), although a cardueline, forages for small seeds on the ground (Austin, 1968), like an emberizine. Likewise, crossbills (*Loxia*: Carduelinae) forage for relatively small seeds, but in conifer cones (Benkman, 1988a), and in winter require seed encounter rates similar to those required by emberizines (Benkman, 1988b). Crossbills, however, forage in trees, but are often exposed at the tips of branches. Consequently, the rosy finch and crossbills are analysed separately from the other carduelines.

All the other finch taxa analysed forage for seeds mostly on the ground: *Geospiza* (Grant, 1986; Schluter, 1988a,b); Passeridae (Schluter, 1988a,b); Drepanidinae (S. Conant, personal communication).

Methods

I used digital calipers to measure bill depth on five male and five female specimens of each of 12 species from the Carduelinae and 11 species of the Emberizinae at the American Museum of Natural History. Bill depth was the greatest measured depth at the base of the bill. Mean body mass, sexes combined, was obtained from Dunning (1984), Pulliam (1985) and Benkman (1988a). I measured specimens mostly from the same subspecies and geographical location for which there were body mass data. Bill depth and body mass measurements for the other taxa were obtained from various sources; Passeridae (D. Schluter, personal communication), Drepanidinae (Conant, 1988; Weathers and van Riper, 1982; S. Conant, personal communication; P. R. Grant, personal communication), *Geospiza* (Abbott *et al.*, 1977; Smith *et al.*, 1978; Grant *et al.*, 1985): the populations chosen represented mostly granivorous populations (P. R. Grant and B. R. Grant, personal communication), *Fringilla* (Grant, 1979), *Junco hyemalis insularis* (Power, 1980; B. D. Cutler and L. F. Baptisa, personal communication) and *Carpodacus mexicanus amplus* (Power, 1980). I only analysed Passeridae from the Kenya finch community because most of the Estrildidae have red bills suggesting sexual selection on bills (see Discussion). To minimize such an effect, I only analysed Passeridae with pale or dark bills.

I use major axis regressions to provide the best functional relationship between body mass and bill depth (Sokal and Rohlf, 1981; Pagel and Harvey, 1988). Because each species within a subfamily is not strictly independent, statistical comparisons are problematic (Pagel and Harvey, 1988). I use a binomial test to determine whether overall the patterns are consistently repeated between taxa.
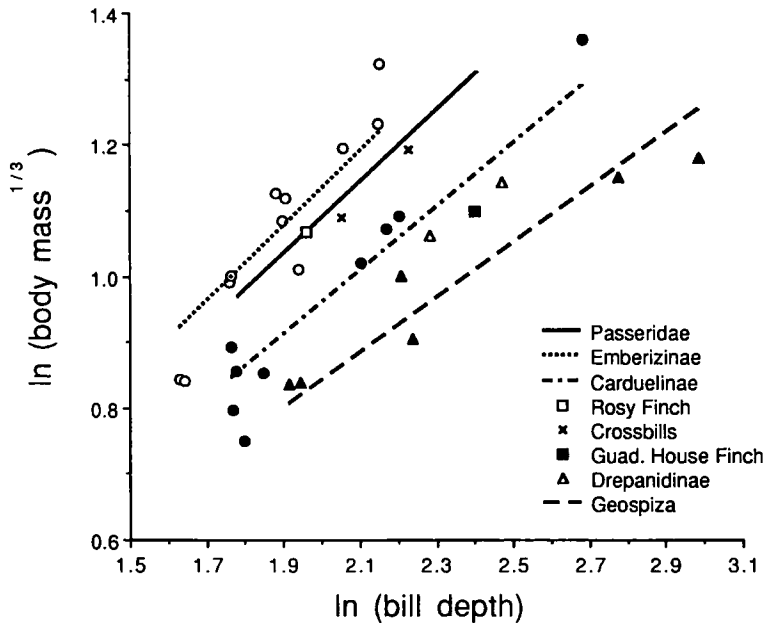
Figure 1. The relationship between body mass (g) and bill depth (mm) for 12 species of Carduelinae (●), 11 species of Emberizinae (○), 6 species of *Geospiza* (▲), 13 species of Passeridae, and 2 species of Drepanidinae. To reduce clutter, only the regression line is presented for Passeridae. The lines represent best-fit major axis regressions. The major axis regression equations (and 95% confidence limits to the slope), where Y is the natural logarithm of the cube root of body mass and X is the natural logarithm of bill depth, are the following: carduelines, $Y = -0.0054 + 0.4824X$, $(0.4587 - 0.5066$, excluding the rosy finch and crossbills); emberizines, $Y = -0.0043 + 0.5685X$, $(0.5459 - 0.5916)$; *Geospiza* $Y = 0.0054 + 0.4176X$, $(0.4140 - 0.4212)$; and Passeridae $(Y = -0.0030 + 0.5459X$, $(0.5178 - 0.5746)$. The 11 species of emberizine and the state(s) or province(s) from which specimens were weighed and collected, listed in order of increasing body mass, are: *Spizella pusilla* (PA,NY), *Spizella passerina arizonae* (AZ), *Junco h. hyemalis* (PA), *Spizella a. arborea* (MA,NY), *Melospiza m. melodia* (PA,NJ), *Zonotrichia albicolis* (PA,NY), *Z. atricapilla* (CA), *Z. l. leucophrys* (PA,SD,MN,WI,Sask, Ont,NS), *Z. querula* (KA,Man,NWT), *Pipilo e. erythrophthalmus* (PA,NY,CN,NJ) *P. fuscus crissalis* (CA). The 12 species of Carduelinae and the state(s) or province(s) from which specimens were weighed and collected, listed in order increasing body mass, are: *Carduelis lawrencei* (CA), *C. psaltria* (CA), *C. tristis* (PA,NY), *C. f. flammea* (AK,BC,Ont), *C. pinus* (PA,NY), *Carpodacus mexicanus* (CA,NY), *Leucosticte arctoa dawsoni* (CA), *Carpodacus p. purpureus* (PA,NY), *Loxia leucoptera* (AK,NB), *Carpodacus cassinii* (AZ,NM), *Loxia curvirostra bendirei* (NY,AZ, Alta), and *Coccothraustes v. vespertinus* (PA,NY,MN,IA). The data for *Geospiza* are from the islands Genovesa, Daphne Major, and Española. The two species of Drepanidinae are *Psittirostra cantans* and *P. ultima*.

Results

Within North America, ground-foraging emberizines are predicted to have relatively larger body masses than tree- and shrub-dwelling carduelines. As predicted, body mass tends to increase more rapidly with bill depth for emberizines than for carduelines (Fig. 1).

Differences in predator vulnerability may have caused differences in body mass relative to bill size within the carduelines. The rosy finch (Carduelinae) forages for small seeds on the ground (Austin, 1968), like an emberizine, and the ratio of its body mass to bill depth is more similar to that

of emberizines than carduelines (Fig. 1). Crossbills also forage for small seeds, and for their bill depth, have relatively large bodies compared to other carduelines (Fig. 1; see also Benkman, 1988a). There is also a fair amount of scatter among the small-billed carduelines, representing five species of *Carduelis*. Whether this variation is related to vulnerability to predators is not clear.

Body mass increases with bill depth in a similar manner for both ground-foraging finch taxa (North America, Emberizinae, $m = 0.568$; Kenya, Passeridae, $m = 0.546$) (Fig. 1). The similarity in slope suggests convergence between different ground-foraging taxa on continents where predators are common.

Finches on the oceanic islands of Hawaii and the Galápagos, where predators are rare, have relatively small bodies compared to finches on the mainland (Fig. 1). The two drepanids on Hawaii have relatively small bodies compared to Carduelines (Fig. 1), although they have relatively larger bodies than *Geospiza* from the Galápagos (Fig. 1). Avian predators, however, were probably more common on the Hawaiian Islands prior to the arrival of Polynesians (Olson and James, 1982), than on the Galápagos. These analyses and visual inspection of Fig. 1 demonstrate a progressive increase in body mass relative to bill depth, especially the slope (m) of the relationship, with the presumed increase in predation pressure from the island-dwelling *Geospiza* (0.418) to the ground-foraging Passeridae (0.546) and emberizines (0.568), with tree- and shrub-dwelling carduelines (0.482) being intermediate in morphology and presumed predation.

Additional comparisons were made between finch species that have differentiated on islands or island groups and their congeners or conspecifics on the mainland. On the California Channel Islands and Guadalupe Island there are endemic house finch (*Carpodacus mexicanus*: Carduelinae) populations. Bird-eating *Accipiter* hawks are absent from Guadalupe Island (Howell and Cade, 1954) and, as would be predicted, the Guadalupe Island house finch (*C. m. amplus*) has a lower ratio of body mass (cube root) to bill depth than conspecifics on the mainland (Power, 1980). In fact, the ratio of body mass to bill depth of the Guadalupe house finch has converged on those for Drepanids (considered to be derived from Carduelinae; see Discussion) on Hawaii (Fig. 1). *Accipiter* hawks are present on the California Channel Islands (Diamond and Jones, 1980) and the house finches on these islands, although differing in bill depth from mainland populations, have similar ratios of body mass (cube root) to bill depth as mainland populations (Power, 1980). On Guadalupe Island there is also an endemic population of dark-eyed junco (*Junco hyemalis insularis*: Emberizinae). Indeed, the ratio of body mass (ln of cube root) to bill depth (ln) of the Guadalupe junco (0.52) is less than that for mainland juncos (0.56).

On both the Azores and Canary Islands there are no resident hawks (Bannerman, 1963; Bannerman and Bannerman, 1966) and the chaffinch (*Fringilla coelebs*: Fringillidae) has differentiated from the mainland form (Grant, 1979). The chaffinch on the Azores (*F. c. moreletti* on Sao Miguel) has a smaller ratio (0.65) of body mass (ln of cube root to bill depth (ln)) than the chaffinch on the Iberian Peninsula (0.71). On the Canary Islands the chaffinch has differentiated into both a distinct species (bluefinch, *F. teydea*) and, from an apparent second invasion, into a distinct subspecies (*F. c. tintillon*) (Grant, 1979). As predicted, the bluefinch (on Tenerife) has a smaller ratio of body mass to bill depth (0.62) than the chaffinch in North Africa (0.67), but *F. c. tintillon* (on Tenerife) has a larger ratio (0.69). This latter case may provide a counter-example to the usual trends of relatively smaller bodied finches where predators are rare, however, *tintillon* apparently forages mostly for insects as suggested by its relatively long bill (Grant, 1979).

In all eight of the above comparisons, excluding the *Fringilla* on the Canary Islands where the trend is equivocal, body mass relative to bill depth is larger for finches that are more vulnerable to predators. Assuming an equal probability for body mass to be larger as smaller for finches more vulnerable to predators, the overall pattern is significant (binomial test, $p = 0.004$).

Additional comparisons that appear consistent with the above patterns, but for which body mass data were unavailable, include parrot-finches (*Erythrura*: Estrildidae). For example, based on text and drawings in Goodwin (1982) and Pratt *et al*. (1987) seed-eating parrot-finches in southeast Asia and New Guinea (e.g. *E. trichroa*) have relatively large bodies compared to parrot-finches confined to small islands in the South-Pacific lacking hawks (e.g. *E. cyaneovirens*).

Discussion

The increase in body size, relative to bill size, with increases in vulnerability to predators is consistent with the hypothesis that increased body size enhances predator evasion (Schluter, 1988a). Conversely, as predation pressure is relaxed body size decreases relative to bill size. A small body minimizes metabolic demands and a larger bill can more efficiently handle a wider range of seed sizes (Newton, 1967; Grant *et al*., 1976; Pulliam, 1985; Benkman and Pulliam, 1988).

I will now consider four alternative hypotheses for differences between taxa in body size relative to bill size (see Schluter [1988a,b] for a more detailed discussion of alternative hypotheses underlying differences between Kenya and Galápagos finch communities). One hypothesis is that larger body size improves tolerance to cold and resistance to starvation (Calder, 1974). This hypothesis, however, can be rejected as a general explanation for the differences in body size among groups. Both Kenya and Galápagos finches live near the equator and experience similar climates (Schluter, 1988b), yet differ significantly in body size relative to bill size (Schluter, 1988a). Furthermore, carduelines have relatively smaller bodies, but, in general, occur farther north than emberizines. Nevertheless, some body size differences may be related to cold tolerance and resistance to starvation. Among ground-foraging finches on continents, equatorial Kenya finches tend to have smaller bodies relative to bill size than temperate emberizines. Similarly, within the genus *Carduelis* (Carduelinae), body size tends to increase with increases in latitude. Thus, some of the minor differences between and within groups may be related to resistance to starvation, but the major overall differences are inconsistent with this hypothesis.

A second hypothesis is that body size is limited by habitat productivity, with larger bodied birds for a given bill size occurring in more productive habitats. This hypothesis is inadequate for explaining why Kenya finches have relatively larger bodies than Galápagos finches. The two areas have similar seed densities (D. Schluter and R. Repasky, personal communication) and similar seed size distributions (Schluter, 1988a,b). Moreover, there are more non-finch seed consumers in Kenya than in the Galápagos (Schluter, 1988b), and thus less seed should be available for finches in Kenya than in the Galápagos. Data are inadequate for making similar comparisons among the other groups. Neither of these first two hypotheses predict differences between taxa in the slopes of relationship between body size and bill size.

A third hypothesis is that because of phylogenetic relationships the different groups of finches differ in their relationships between bill and body size. Different relationships could arise if, for example, there are structural differences between the bills of the different taxa. Structural differences in bills could arise if bill size is subjected to sexual selection. For instance, in the Kenya finch community two species in the Passeridae have red bills. In fact, one of them has a bill depth that lies on the regression line for *Geospiza*. This suggests that at least in some species bills are enlarged because of sexual selection (Goodwin, 1982). Such an effect was minimized by only analysing finches with pale or dark bills.

The phylogenetic constraint hypothesis, however, is inconsistent with the tremendous variation within carduelines (Fig. 1). Other differences are also unlikely to be a result of phylogenetic constraints. For instance, seed-eating finches on the Hawaiian Islands, which are derived from

carduelines (Sibley and Ahlquist, 1982), have converged on *Geospiza* (Fig. 1; Schluter, 1988a). In addition, the ancestor of the *Geospiza* that colonized the Galápagos was probably an emberizine (Grant, 1986). That the ratio of bill to body size is liable to selection in these groups is supported by the tremendous radiation in bill and body sizes within the Galápagos finches (Geospizinae; Grant, 1986) and Hawaiian honeycreepers (Drepanidinae; Raikow, 1977).

Fourth, birds prefer to forage in safe locations (e.g. Caraco *et al.*, 1980) and, because large body size enhances dominance (Gauthreaux, 1978) which influences access to safe feeding sites (e.g. Schneider, 1984; Ekman and Askenmo, 1984; Ekman, 1987), increased vulnerability to predators may intensify selection for larger body size to improve access to safe feeding sites. This hypothesis makes similar predictions to those of Schluter's predator evasion hypothesis. The amount and importance of intra- and interspecific dominance interactions in determining foraging location and vulnerability to predators requires additional study. Preliminary studies indicate that dominance interactions influence foraging location in emberizines (Davis, 1973; Schneider, 1984), with larger bodied species foraging closer to cover (Pulliam and Enders, 1971; Davis, 1973; Pulliam and Mills, 1977; Pulliam, 1983). In contrast, among *Geospiza* dominance interactions are infrequent and appear to be of minor significance (P. R. Grant, personal communication). Although neither of the two predator avoidance hypotheses can be rejected, nor are they mutually exclusive, selection for large body size to improve access to safe feeding sites may be more general to other bird communities (e.g. parids; J. Ekman, personal communication), and possibly mammals (e.g. Dickman, 1988).

In sum, all of these factors, including cold tolerance and starvation resistance, habitat productivity, foraging substrate, phylogenetic constraints, and vulnerability to predators, probably affect body size. Indeed, other factors may also influence the slope of the curve representing the relationship. For example, the method of predator evasion may vary with body size. In emberizines some of the smaller species rely more on crypsis, whereas the larger species fly to cover to evade predators (Pulliam and Mills, 1977). However, only the affect of vulnerability to predators is consistent with the major differences in body size to bill size relationships within and among groups.

Seed-eating finches are particularly susceptible to predators because adaptations for capturing and handling seeds are not conducive for evading predators. Rapid and manueverable flight does not improve seed capture, but is important for evading predators. A massive bill improves seed handling ability, but may reduce aerodynamic efficiency. Hence, the optimal seed-eating finch may approximate a 'flying bill' (H. R. Pulliam, personal communication; Newton, 1967) in the absence of predators, but differs from the optimum in the presence of predators. The morphology of other seed-eating birds, such as parrots, may also be influenced by predator vulnerability. In contrast, the optimal body form for a bird capturing active prey (e.g. flycatchers and swallows) should be similar in both the presence and absence of predators. Predators have probably influenced the morphology of other types of birds, especially taxa that spend most of the day foraging for inactive prey. However, detecting the impact of predators in groups other than seed-eating finches (and parrots?) will probably require more sophisticated analyses than those used above.

Predation and resource partitioning

Seed size partitioning is strongly evident for *Geospiza* (Grant, 1986; Schluter, 1988a,b) and carduelines (Newton, 1967, 1972; Benkman and Pulliam, 1988), but not for emberizines (Pulliam and Enders, 1971; Pulliam, 1983, 1985; Pulliam and Dunning, 1987) or Kenyan finches (Schluter, 1988a,b). I hypothesize that this difference arises indirectly because of differences between taxa in vulnerability to predators: the presence of predators favours large bodies relative to bill sizes

which in turn reduces the potential for seed size partitioning. There are two reasons assemblages of finches with relatively large bodies are less able to partition seed sizes.

First, increased body size, particularly for large-billed species, reduces seed size partitioning because energetic constraints on larger billed, and hence larger bodied, birds are increased. As a result, large-billed finches may be absent from communities where vulnerability to predators is high. Consequently, the range of bill sizes in emberizines is smaller (Fig. 1) and they consume a smaller size range of seeds than do carduelines (Benkman and Pulliam, 1988; Pulliam, 1985; Schluter, 1988a,b). In fact, because of predators, natural selection may favour alternative strategies for foraging on large loose seeds. This may be why ground-feeding birds on continents that consume large-seeds are non-passerines, such as quail and doves (e.g. Schluter, 1988a). These species reduce the risk of predation in two ways: (1) they reduce time spent exposed on the ground foraging by quickly gathering seeds without husking them and storing them in large crops; (2) they may be better able to evade predators because they have large bodies relative to their bill sizes and their muscular gizzard, located near their centre of gravity, grinds up the seeds.

Second, large body size increases metabolic demands which may reduce the number of seed sizes that can be utilized (Pulliam, 1985). Consequently, fewer large-bodied species can be supported by a given seed size distribution than can small-bodied species with a similar bill size range. Indeed, larger emberizine species are only added to communities as seed densities increase (Pulliam, 1983, 1985) and there is little evidence that seed size partitioning is common among emberizines in North America (Pulliam and Enders, 1971; Pulliam, 1983, 1985; Pulliam and Dunning, 1987; Benkman and Pulliam, 1988) or among Kenya finches (Schluter, 1988a,b). Emberizines partition the environment by selecting different habitats and distances to cover, apparently to avoid predation (Davis, 1973; Pulliam and Mills, 1977; Lima *et al.*, 1987). In contrast, seed-size distributions are a much more important factor influencing the species composition of *Geospiza* communities than are seed densities (Schluter and Grant, 1984; Grant, 1986).

Acknowledgements

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