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THE COMPARATIVE FEEDING RATES OF NORTH AMERICAN SPARROWS AND FINCHES[1]

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Abstract. Data on the seed profitabilities (mass of seed ingested per unit time) of captive emberizine sparrows and cardueline finches were used to interpret the underlying factors promoting differences in their ecologies. Sparrows consume seeds that are approximately an order of magnitude smaller in size that those consumed by finches of similar body mass. Because sparrows consume such small seeds and because finches are much more efficient at handling large seeds, sparrows need to encounter seeds at rates that are one to two orders of magnitude greater than that required by finches. As a result, sparrows have to spend much more time foraging than do finches, and sparrows are not able to go for as long periods of time searching for new food patches as are finches. Consequently, sparrows are relatively sedentary and restricted to areas of dense seed concentrations, whereas finches are extremely vagile and move over very large geographic areas in search of new patches of food. Furthermore, resource partitioning is more pronounced among finches. Small and large finch species eat very different seed sizes, whereas the diets of small and large sparrows overlap greatly.

Key words: Carduelinae; Emberizinae; encounter rates; finches; foraging behavior; profitability; resource partitioning; seed handling time; sparrows.

INTRODUCTION

The rate at which energy can be acquired influences every aspect of the ecology of vertebrates, from social organization (e.g., Caraco et al. 1980) to community structure (e.g., Werner 1977, Pulliam 1985). In seed-eating finches, the rate of energy acquisition is closely related to the time required to husk or handle seeds once they have been located. In previous studies, we measured the seed handling times of both emberizine sparrows and cardueline finches to interpret patterns of food use and resource partitioning (Pulliam 1985; C. W. Benkman, *personal observation*). In this paper, we present and compare the data, and show how differences in seed handling abilities between these two groups are associated with differences in their resource exploitation strategies.

Although both emberizine sparrows (hereafter sparrows) and cardueline finches (hereafter finches) have conical bills, sparrows differ from finches in regard to other morphological characteristics (Tordoff 1954, Raikow 1978) and biochemistry (Avise et al. 1980, Marten and Johnson 1986). These differences result in sparrows and finches being classified in different families; sparrows are in the Emberizidae and finches are in the Fringillidae. In this paper, we discuss some dramatic differences in the foraging ecology of the two groups that occur despite their superficially similar appearances.

METHODS

Details on the experimental procedures have been presented elsewhere (Pulliam 1985); therefore only brief descriptions are given here.

Sparrows

The sparrow species used in the experiments were Chipping Sparrow (*Spizella passerina*) (13 g), Dark-eyed Junco (*Junco hyemalis*) (20 g), and White-crowned Sparrow (*Zonotrichia leucophrys*) (23 g). These birds were housed in indoor aviaries and their diet consisted of mixed seeds, fruit, lettuce, mealworms, and vitamin-enriched water.

Seeds used in the experiments with sparrows were collected at The Audubon Research Ranch near Elgin, Arizona. The sparrows always had prior experience with each species of seed used in the tests. Because sparrows generally forage for seeds on the ground, we scattered 50 seeds on the floor of the observation cage and placed an individual sparrow in the dark cage in the late afternoon. The light was turned on the following morning and seed handling times were measured.

Handling time for sparrows was measured from the

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time a seed was picked up until the husk fell from the bird's bill. Sparrows usually swallow seed kernels whole. Handling times were initially recorded with an Esterline-Angus event recorder to the nearest tenth of a second; later observations were recorded with an Apple II computer programmed to time and record events to one-tenth of a second. Data were gathered on 1 to 11 individuals of each sparrow species foraging on each seed species (see Pulliam 1985). Because handling times were not measured for all 50 seeds and the number of birds per bird species varied, sample sizes differed between seed species. Each datum represents the mean for a bird species handling an average of 60 seeds (SD = 47).

Samples of both whole kernels (husked mass) and complete seeds (unhusked mass) of each seed species were weighed. In the case of some of the smallest seed species, the mass of the seed coat was so small that the husked and unhusked masses were recorded as the same.

Finches

The finch species used in the experiments were American Goldfinch (*Carduelis tristis*) (13 g), House Finch (*Carpodacus mexicanus*) (21 g), and Evening Grosbeak (*Coccothraustes vespertinus*) (55 g). They too were housed in indoor aviaries but were fed commercial sunflower (*Helianthus* spp.) and niger thistle (*Guizotia abyssinica*) seeds (usually ad libitum, although sometimes food was restricted if birds gained in mass), and vitamin-enriched water.

Seeds used in the experiments were eight size classes of commercial sunflower and niger thistle seeds with individual unhusked seed masses ranging from 2.3 to 117.5 mg. Sunflower and thistle seeds were chosen because composite (Compositae) seeds are an important food for many finches in nature (Martin et al. 1951, Newton 1967, 1972, Austin 1968).

During seed-handling time tests, 10 preweighed seeds were placed in a partially covered plastic tray that was attached to a perch in an observation chamber. Because finches, unlike sparrows, normally forage within vegetation above the ground (Newton 1967), the birds were required to handle seeds while perched. The food tray was designed so that kernels dropped by the birds while handling seeds fell through a screen to the floor where the kernels could not be retrieved by the birds. An individual finch was held overnight in the chamber without food for at least 16 h prior to the seed-handling experiments the following morning.

Handling time for finches was defined as the interval from when a seed was picked up until no part of the seed was being manipulated in the bill (mandibulated). In contrast to sparrows, finches often broke and mandibulated the kernel before swallowing; thus handling time was usually longer than husk removal time alone. Handling times were recorded with an Apple II computer programmed as an event recorder. To determine the amount of kernels consumed, all seed remains were removed and weighed. Initially both kernel and husk remains were weighed separately, but the husks were not consumed in any measurable amount. Thus, the average mass of kernel consumed per seed was obtained by subtracting seed remains from initial mass. Data were gathered on four individuals of each species. Each datum presented represents the mean for a given individual handling an average of 14 seeds (SD = 6).

Necessary seed encounter rates

The seed-handling efficiency data for both sparrows and finches were used to estimate the rate at which seeds must be encountered to meet energetic requirements. We solved for the necessary encounter rate (λ) for each seed size to match the intake rate required to meet the daily energy expenditure (*DEE*) as follows:

$$DEE = 3.6 \times 10^4 \frac{S}{h + 1/\lambda}.$$

DEE was estimated using the equation: $\ln(DEE) = 2.57 + 0.61\,(\ln[M])$, where *DEE* equals the total daily expenditure in kilojoules and M is the mass of the bird in grams (Walsberg 1983: Equation 8). Ten hours (3.6×10^4 s) was assumed the maximum time available to forage during a midwinter day in southern Arizona, where all six bird species occur in winter (Phillips et al. 1964). Midwinter was chosen because this is when diets consist mostly of seeds (Martin et al. 1951) and winter is the period when food is thought to be most limiting (Newton 1967, Fretwell 1972, Pulliam and Parker 1979). S is a product of mass (in milligrams) of kernel consumed per seed, specific energy value (joules per milligram) of the kernel, and assimilation efficiency. We assumed that the kernels of seeds commonly consumed by sparrows have 20 J/mg (Kendeigh and West 1965) and those eaten by finches have 23 J/mg (Grodzinski and Sawicka-Kapusta 1970). Assimilation efficiencies were assumed to be 75% (Willson and Harmeson 1973 and references therein). h is handling time, in seconds, which we measured. We solved for $1/\lambda$.

RESULTS

Table 1 gives regression equations for seed handling time as a function of mass of kernel consumed. The intercepts and slopes of the equation for Chipping Sparrows differed significantly ($P < .05$) from those for juncos or White-crowned Sparrows, but there was no significant difference between the intercepts or slopes of the latter two species. Among finches the intercepts for goldfinches and grosbeaks were the only ones significantly different ($P < .05$). The slopes, however, differed significantly ($P < .05$) among all three finches. The slope for the grosbeak was significantly smaller than those of both the House Finch and goldfinch, and the slope for the House Finch was significantly smaller than that for the goldfinch. This implies that as seed

TABLE 1. The relationships between the natural logarithm of seed handling time (h) and kernel mass consumed (x) for three species of emberizine sparrows and three species of cardueline finches.

Species	Regresssion equation	n	r^2
Chipping Sparrow	$\ln(h) = -1.18 + 3.26x$***	18	0.66
Dark-eyed Junco	$\ln(h) = -0.49 + 1.60x$*	5	0.79
White-crowned Sparrow	$\ln(h) = -0.40 + 1.36x$†	6	0.53
American Goldfinch	$\ln(h) = 1.13 + 0.12x$***	14	0.72
House Finch	$\ln(h) = 1.41 + 0.03x$***	19	0.76
Evening Grosbeak	$\ln(h) = 1.54 + 0.01x$***	19	0.48

† $P = .096$, * $P < .05$, *** $P < .001$.

size increases, the relative seed-handling efficiencies of large finches increases.

All the intercepts were significantly smaller for sparrows than for finches ($P < .05$), yet the slopes were all significantly larger for sparrows than for finches ($P < .05$). These results imply that sparrows handled small seeds more efficiently than finches, but on larger seeds finches were relatively more efficient. By setting the handling times (h) for sparrows equal to those for finches and solving for x, we determined that sparrows were more efficient than finches at handling seeds <0.74 mg, and that finches were more efficient than sparrows at handling seeds >1.44 mg.

To meet midwinter daily energy requirements, sparrows must encounter a seed at least once every 2–5 s when not actually handling them (Fig. 1a). Whether sparrows differ among themselves in efficiency in relation to the seed sizes is not obvious. The relatively narrow range of seed sizes used in the experiments may have prevented us from detecting a relationship, although in nature sparrows often encounter seeds only in this range (Pulliam and Enders 1971, Pulliam 1985).

Given that all seed sizes are available, finches require much lower encounter rates than do sparrows (compare a and b of Fig. 1). Sparrows must find and consume, on average, one seed every 1–5 s throughout a 10-h day. On the other hand, goldfinches need to procure a seed, on average, every 100 s, and House Finches and grosbeaks need to encounter a seed every 200–500 s. In further apparent contrast to sparrows, each finch species has a different seed size range for which it is most efficient. At the smallest seed sizes (<25 mg) goldfinches are the most efficient, in that they can exist on lower seed encounter rates or seed densities, given that all three finches are equally efficient at finding and procuring these seeds. An analogous interpretation can be given for medium seed sizes (25–65 mg), but for this seed size range the House Finch is most efficient. Only the grosbeak can survive on the largest seed sizes (≥90 mg).

DISCUSSION

Adequacy of commercial seeds

Although our experiments with finches were conducted with commercial seeds, data on comparably sized cardueline finches in Europe (Newton 1967, 1972) support the results we found. The European Goldfinch (*Carduelis carduelis*) approximates the size of the American Goldfinch (16 g, 7.5 mm bill depth, 12.4 mm bill length compared to 13 g, 7.4 mm bill depth, 10.2 mm bill length, respectively), and the former consumes seeds ranging in size from 0.05 to 50 mg. Data in Fig. 1b indicate a similar seed size range for the American Goldfinch. Unfortunately, Newton does not provide the relative contributions of the different seed

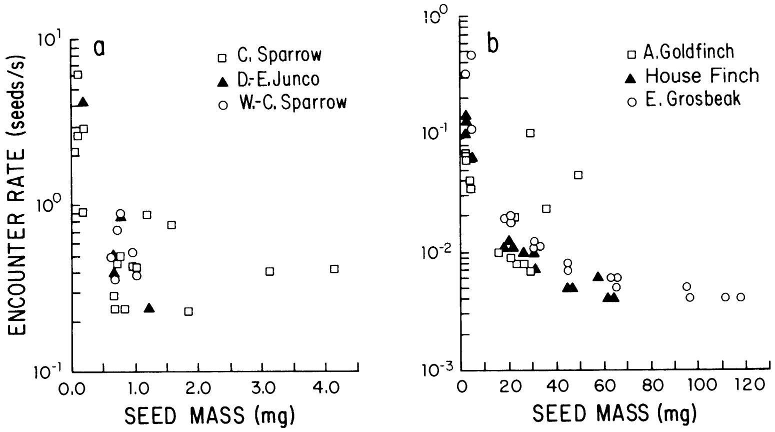

FIG. 1. The estimated necessary seed encounter rates for (a) three species of emberizine sparrows and (b) three species of cardueline finches to meet their estimated daily energy requirements. Note the different values on the axes.

sizes to the diet. The Greenfinch (*Carduelis chloris*) is of comparable size to the House Finch (29 g, 11.5 mm bill depth, 13.1 mm bill length compared to 21 g, 9.1 mm bill depth, 13.1 mm bill length, respectively). Greenfinches consume seeds ranging from 0.1 to 230 mg, which is a size range considerably larger than would be expected given the data in Fig. 1b. However, Greenfinches consume seeds mainly between 10 and 100 mg, which is consistent with the data presented for House Finches (Fig. 1b). Nevertheless, if a different seed type had been used in the seed handling experiments, a different seed size range would likely have been found. Greater correspondence between the data on the two goldfinches may have resulted because European Goldfinches consume mostly seeds from composites (76% of their diet by mass). The Hawfinch (*C. coccothraustes*) is nearly identical in size to the Evening Grosbeak (55 g, 17.7 mm bill depth, 20.5 mm bill length as compared to 55 g, 14.8 mm bill depth and 20.3 mm bill length, respectively). Newton found that Hawfinches consume seeds mostly >100 mg in mass (68% of diet by mass) and that seeds between 10 and 100 mg make up most of the rest of the diet. These data are consistent with those presented for Evening Grosbeaks in Fig. 1b. In sum, although the data on captive finches are based on commercial seeds, diet data gathered in the field on finches of similar size in Europe suggest that our results are robust.

General Discussion

In North America, many sparrows and finches feed predominantly on seeds, especially in winter (Martin et al. 1951). Yet, the ecologies of these two groups differ markedly (e.g., Phillips et al. 1964). Sparrows forage on the ground mostly for grass and forb seeds. Finches, on the other hand, forage for seeds mostly on conifers and dicotyledonous trees, shrubs, and herbs. Differences between these two groups of resources and the means by which they are efficiently exploited influence the morphologies, behaviors, and ecologies of sparrows and finches.

Seeds available in habitats occupied by sparrows in winter, such as in the old fields of the southeastern United States and the grasslands of southeastern Arizona, are mostly <5 mg (Pulliam and Enders 1971, Pulliam 1985); this size range is similar to that reported for seeds of most annual and perennial herbaceous plants in California (Baker 1972). The seeds consumed by sparrows are also quite cryptic (T. Getty, *personal communication*). Nonetheless, sparrows must find seeds every 2–5 s to survive. Thus, sparrows must occupy habitats containing high densities of seeds. The high seed encounter rates required by sparrows feeding solely on very small seeds limits their ability to exploit patchy seed supplies because long diurnal flights in search of new patches are not a feasible option; most of the day must be spent foraging. Moreover, sparrows may not be able to gather sufficient seed to survive the short winter days at higher latitudes.

Finches are more efficient than sparrows at handling seeds >2 mg and frequently consume seeds that weigh well over 10 mg (Newton 1967, 1972); seeds of many native shrubs and trees in California weigh >10 mg (Baker 1972). Finches have more massive jaw musculature than sparrows (W. J. Bock, *personal communication*), which is one reason finches can handle larger seeds more efficiently.

Not only do finches consume a wider range of seed sizes than do sparrows, but the diversity of seed shapes may also be greater, and if so this would require more diverse bill structures to handle the seeds efficiently. The seeds consumed by finches are very apparent, and their defenses against avian seed predators often consist of tough seed coverings. For example, we have calculated that the coverings of the seeds of the dicotyledonous plants listed in Pulliam (1985) make up a greater proportion of the total seed mass and increase more rapidly as seed size increases than is the case for monocotyledonous plants. The relationships are $y = 1.66x^{3.21}$, $r^2 = 0.88$, $n = 7$, and $y = 0.45x^{1.35}$, $r^2 = 0.59$, $n = 11$, for dicotyledonous and monocotyledonous plants, respectively, where y is seed cover mass and x is kernel mass, both in milligrams.

The ability to handle large seeds efficiently enables finches to exist at low seed densities because seed encounter rates do not need to be high. Finches can survive even when they encounter a seed every 100–500 s. Moreover, even though finches can rapidly process large seeds, satiation is delayed because they have large structures in which to store seeds (e.g., esophageal diverticula in *Carduelis* and *Loxia* [Fisher and Dater 1961], buccal pouches in *Pinicola* and *Leucosticte* [Miller 1941, French 1954]). These seed-storing structures are probably essential for finches to exploit concentrated but widely scattered food patches. These seed-storage structures also enable finches to carry large quantities of seed to their nestlings (Newton 1972). In winter, finches often move long distances between food plants. Once at a food plant or group of food plants, finches rapidly consume seeds over relatively brief time periods (C. W. Benkman, *personal observation*). This ability to exploit concentrated food patches rapidly enables finches to utilize seed resources that are patchily distributed. Further, when fed ad libitum in the laboratory in winter, sparrows do not increase much in body mass, but finches often gain several grams and may even increase their body mass by over a third (C. W. Benkman and H. R. Pulliam, *personal observations*). This apparently facultative ability to gain mass by finches facilitates exploitation of patchy food resources.

Seed production varies annually in many of the plants utilized by finches (Bock and Lepthien 1976; also see Janzen 1971, Silvertown 1980). Because seed abundances can be extremely variable both annually and spatially, the ability of finches to spend large parts of the day searching for areas of abundant seed may be crucial to their survival. The ability of finches both to handle and process greater amounts of seed than can sparrows, enables finches to winter in more northerly latitudes.

The narrow range of seed sizes utilized by sparrows, in combination with the limited diversity of structural defenses of the seeds, has reduced the potential for seed size partitioning among sparrows. Finches, however, utilize both a wider range of seed sizes and seeds that have more robust physical defenses. This allows different finch species to specialize on different seed sizes, but specialization on one particular seed size in turn reduces the efficiency at which other seed sizes can be utilized (Fig. 1b). This provides a mechanism by which finches have been found to partition seed sizes (see Newton 1967, 1972).

In summary, differences between sparrows and finches, both in seed sizes consumed and seed profitabilities, affect their ecologies; sparrows consume smaller seeds and a seed size range that is an order of magnitude smaller than that consumed by finches. Because of differences in seed profitabilities and seed sizes consumed, sparrows are required to find seeds at rates that are 2–3 orders of magnitude greater than that required by finches. Differences in necessary seed encounter rates among sparrows implies little potential for seed size partitioning, but among finches seed size partitioning is likely.

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