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GRIT USE BY HOUSE SPARROWS: EFFECTS OF DIET AND GRIT SIZE[1]

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Abstract. Free-ranging House Sparrows (*Passer domesticus*) were captured with mist nets in central Iowa from August through March, 1990–1993, and their gizzard contents were used to compare grit use by sex, season, and diet. Males and females did not differ in mean grit amounts or sizes (overall mean size = 0.5 mm) in their gizzards. Gizzards of birds captured during March and August contained more grit than those of birds captured during September through February ($\bar{x}$ = 674 vs. 477). Gizzards containing >75% animal material (insects) had more grit than those containing >75% plant food ($\bar{x}$ = 681 vs. 531). Aviary experiments then were conducted with captive House Sparrows to evaluate the effects of diet and grit size on grit choice and retention. When birds were given grit particles 0.2–1.4 mm in size and either soft animal food (canned dog food) or hard plant food (wild bird seed), grit in gizzards of birds on the two diets did not differ in mean number or size. When birds were given both animal and plant food and either small (0.2–0.4 mm) or large (1.0–1.4 mm) grit, gizzards of birds consuming small grit contained 5 times more particles than those of birds consuming large grit ($\bar{x}$ = 275 vs. 51). In experiments evaluating grit retention, most grit in gizzards was replaced within five days. Grit replacement rates were unaffected by diet, but birds given only hard, plant food averaged more grit per gizzard than those given only soft, animal food ($\bar{x}$ = 538 vs. 205). Gizzards of House Sparrows given only small grit consistently retained grit longer and contained more particles ($\bar{x}$ = 853 vs. 174) than those of birds given only large grit.

Key words: Diet; gizzard; grit use; House Sparrow; Passer domesticus; *Iowa.*

INTRODUCTION

Despite a long history of interest in the avian gizzard and its function (e.g., Borelli 1743, Réaumur 1756, Spallanzani 1783 [all cited in Farner 1960]), relatively little is known about the process and dynamics of grit use by birds. Grit use is widespread among birds (Meinertzhagen 1954, 1964; Best and Gionfriddo 1991), and the value of grit in increasing avian digestive efficiency has been demonstrated (Fritz 1937, Lienhart 1953, Titus 1955, Smith 1960). Grit also is known to provide supplementary calcium and other minerals which may be critically important to granivores and other species with low-calcium foods (McCann 1961, Harper 1963, Harper and Labisky 1964, Korschgen 1964, Norris et al. 1975). Little information is available, however, regarding the factors that influence grit use.

The amount of grit used by birds may be influenced by grit size and bird diet. Within a species, an inverse relationship sometimes exists between mean grit size and the number of grit particles in the gizzard (Alonso 1985, Best and Gionfriddo 1991), indicating that birds consuming smaller grit generally use more particles. Because birds use grit to improve mechanical grinding of food in the gizzard, the value of (and need for) grit should vary with diet. Several authors have noted greater grit use when diets consist of hard, coarse foods such as seeds and other plant material (Porkert 1972, Norris et al. 1975, Bishton 1986, Hogstad 1988). Some avian digestive systems are adapted to enable birds to exploit different amounts and types of foods seasonally. For example, some species regulate digestive efficiency by seasonal changes in gut length (Dykstra and Karasov 1992) or by processing different foods at different rates (e.g., Levey and Karasov 1989, 1992). Adaptive, seasonal variation in grit use might be expected to accompany seasonal shifts in the diets of some avian species.

The amounts and characteristics of grit in bird gizzards depend, not only on selection of grit particles by the birds, but also on retention of at least some of those particles in the gizzard. Retention of individual grit particles is influenced by the rate at which grit is ingested (McCann 1939, Smith and MacIntyre 1959, Tagami 1974,

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Trost 1981). When birds have free access to grit, they may consume and eliminate considerable amounts daily (Lienhart 1953; May and Braun 1973; Alonso 1985; Gionfriddo, pers. observ.). On the other hand, birds suddenly deprived of grit can reduce their output of grit and retain particles in their gizzards for long periods (Smith and Rastall 1911, Kraupp 1924, McCann 1939, Walter and Aitken 1961). Other factors, including grit size and diet, also may influence grit retention in the gizzard. Some particles may be retained longer than others because of their size (Smith 1960, Roland et al. 1972, Tagami 1974). Diet can affect retention in several ways. For example, coarse, hard diets may increase the grit ingestion rate and thereby reduce retention (Trost 1981). Hard diets also may reduce grit retention by accelerating grit particle disintegration and elimination (Norris et al. 1975).

In addition to their importance in avian digestion, the dynamics of avian grit use also have direct implications for avian exposure to pesticides. Each year, granular pesticides are applied to millions of hectares of corn and other crops in North America to control agricultural pests (U.S.D.A. 1992). The toxicity of these materials to birds (Balcomb et al. 1984, Hill and Camardese 1984) has generated interest in evaluating avian risk associated with pesticide use. One factor influencing risk is the probability of avian exposure to pesticide granules, and one potential route of exposure is the consumption of granules as a source of grit (Best and Fischer 1992). A clear understanding of the dynamics of grit use by birds is therefore important in assessing avian risk associated with granular pesticide use.

To gain a better understanding of the influence of diet and grit size on avian grit use, we examined grit use by House Sparrows (*Passer domesticus*). First, we characterized natural grit use by free-ranging birds and compared grit use by sex, season, and diet. We then conducted a series of aviary experiments designed to evaluate the influence of diet and grit size on grit choice and retention. The House Sparrow was chosen because it uses a substantial amount of grit (Keil 1973, Pinowska 1975, Best and Gionfriddo 1991) and has a seasonally varying diet. House Sparrows rely heavily on seeds year-round but also consume insects when available (Kalmbach 1940, Gavett and Wakeley 1986). In addition, as ground-foraging granivores (De Graaf et al. 1985), House Sparrows represent the avian feeding guild most likely to be exposed to granular pesticides.

METHODS

GRIT USE BY FREE-RANGING HOUSE SPARROWS

Free-ranging House Sparrows were captured with mist nets from August through March, 1990–1993, at rural sites in Story and Boone counties in central Iowa. Birds were euthanized and taken to the laboratory for analysis of gizzard contents. Each gizzard was sliced in half with a razor blade, and the contents were flushed into a petri dish where they were examined and sorted under a zoom, stereomicroscope. Diet was characterized by visually estimating the percentages (by volume, to the nearest 5%) of plant and animal material. Grit particles were separated from other gizzard contents and counted. Particles < 0.1 mm in size were excluded because they were considered soil material and not grit selected by the birds.

Grit particles in about one-fourth of the House Sparrow gizzards were characterized individually. Gizzards were chosen for this evaluation to include roughly equal numbers of males and females from each season (see below) and from each of six capture locations. The longest and shortest dimensions of each grit particle were measured to the nearest 0.1 mm with an ocular micrometer in the microscope. For each particle, these two values were averaged for an overall measure of grit size. A grit shape index value was calculated for each grit particle by dividing the longest by the shortest dimension. These values were ≥ 1.0, with 1.0 representing a somewhat spherical shape and larger values representing oval to oblong shapes. Grit surface texture was classified into five categories by using a scheme developed by petrologists to describe mineral grains (El-Hinnawi 1966:15). The five surface-texture categories were angular, sub-angular, sub-rounded, rounded, and well-rounded (see Best and Gionfriddo 1991, Fig. 1). An overall mean surface-texture value, the surface-texture index, was calculated for each bird by giving grit particles in the angular category a value of 1, those in the sub-angular category a value of 2, etc.

We tested for seasonal effects on grit use by comparing gizzard contents of birds captured at six rural sites during March and August with those of birds captured at the same locations during September-February. Relatively heavy use of insects by Iowa House Sparrows begins in March and ends in August (Kalmbach 1940; Gionfriddo and Best, unpubl. data). Therefore, although birds were not collected during much of the annual peak in insect activity (April–July), gizzard contents of birds captured in March and August should reflect seasonal patterns of grit-use in response to a diet containing an increased amount of insects. For convenience, we will refer to the March/August collection period as the "insect season" and September–February as the "no insect season." Food in gizzards of most (241 of 245) free-ranging House Sparrows consisted of either >75% plant or >75% animal material, so we examined the influence of diet on grit use by comparing grit from birds that had >75% plant food in their gizzards with grit from those having >75% animal food. Analysis of variance was used to test if interactions among sex, season, and diet affected gizzard grit counts. Two-tailed t-tests were used to determine if mean grit counts, sizes, shape index values, or surface-texture values differed ($P \leq 0.05$) by sex, season, or diet.

EXPERIMENTS

Additional free-ranging House Sparrows were captured throughout the year, fitted with numbered aluminum leg bands, and put in outdoor aviaries where they were held for at least three days (Grit Size and Diet Experiments) or seven days (Grit Retention Experiments) to acclimate to captivity before experiments were begun. During acclimation, birds were provided with the same type of food they later received during experiments.

Before starting each experiment, we anesthetized each bird, inserted a ball-tipped intubation needle into the gizzard, and used a syringe to flush the gizzard with a saline solution. This technique effectively removes all or nearly all food and grit from the gizzards of most House Sparrows (Gionfriddo et al., in press). After recovery from anesthesia, birds were returned to the aviaries and given food, water, and grit. The food and grit provided varied, depending upon the experiment (see below).

Birds assigned (randomly) to a given experimental treatment were housed together in an aviary compartment measuring 3.7 × 4.6 × 2.1 m. The plant diet was a commercially prepared seed mixture (Cardinal Brand Wild Bird Feed, Des Moines Feed Co., Des Moines, IA) containing millet, milo, cracked corn, sunflower seeds, peanuts, and wheat. The animal diet was canned dog food (Grit Size and Diet Experiments: Ken-L-Ration Beef Dinner Dog and Puppy Food, Quaker Oats Co., Chicago, IL; Grit Retention Experiments: Prescription Diet i/d, Hill's Pet Products, Topeka, KS). In each aviary compartment, grit was presented to the birds in two trays, each consisting of a square lumber frame affixed to the concrete aviary floor. The surface (bottom) of each grit tray measured 0.5 m^2, except in the Diet Experiment, in which a relatively large volume of grit necessitated the use of 1.0-m^2 trays. In the Grit Retention Experiments the bottoms of the grit trays consisted of the concrete aviary floor, but in the Grit Size and Diet Experiments, Masonite® was attached to the wooden frames and used as the grit tray bottoms. After each experiment, House Sparrows were euthanized, and gizzards were removed and preserved in 95% ethanol.

GRIT SIZE AND DIET EXPERIMENTS

In the Grit Size Experiment, we gave birds either small or large grit. In one treatment, grit trays contained grit sieved to a size range of 0.2–0.4 mm (representing the lower end of the normal range of grit sizes used by free-ranging House Sparrows [Best and Gionfriddo 1991]). In the other treatment, trays contained grit ranging from 1.0–1.4 mm (upper end of the normal grit size range). Each grit tray was supplied with 25 cc of grit. All birds had access to both hard plant food and soft animal food.

In the Diet Experiment, we gave birds access to either hard plant food or soft animal food. Both groups of birds were supplied with grit representing nearly the entire range of grit sizes normally used by free-ranging House Sparrows (0.2–1.4 mm). To ensure that an *ad libitum* supply of particles of various sizes within that overall range was available to birds, we placed 150 cc of grit in each grit tray.

In both experiments, which were conducted in June, 25 House Sparrows were randomly assigned to each treatment. Grit, which consisted of sand obtained from a sand pit near Ames, Iowa, was replaced in the trays every two days. Both experiments ended after 14 days. Later, gizzard contents were examined, and grit particles were counted and measured (longest and shortest dimensions). Two-tailed t-tests with a significance level of $P \leq 0.05$ were used to compare mean grit counts in gizzards of birds in the paired treatments.

GRIT RETENTION EXPERIMENTS

The Grit Retention Experiments were designed to determine how long individual grit particles are retained in the gizzard and if retention is influenced by diet or grit size. The procedure consisted of giving House Sparrows access to Colorado quartz grit for at least two weeks and then shifting the birds to microcline feldspar grit. (In one experiment the shift was from feldspar to quartz.) Particles of the two mineral types were extremely similar in size, shape, surface texture, color, hardness, and specific gravity. The rates of replacement in gizzards of the first grit type by the second then were determined by euthanizing birds at regular intervals after the shift and examining their gizzard contents.

A preliminary experiment was conducted to determine an appropriate schedule for euthanizing birds after the grit type was changed. The results suggested that replacement (in gizzards) of the first grit type by the second was a slow, gradual process that might take many weeks to complete. Accordingly, in subsequent experiments, we euthanized birds 5, 10, 15, 20, 25, and 30 days after the substitution (in grit trays) of the second grit type for the first. Our main experimental results demonstrated repeatedly (see below) that most grit was replaced in gizzards within five days, and thus, a final experiment (Short Intervals Retention Experiment) was conducted in which birds were euthanized ¼, ½, 1, 2, 4, and 8 days after the grit type was changed.

A critical assumption underlying these experiments was that House Sparrows could not distinguish between quartz and feldspar particles and responded in the same way to the two grit types. It also was assumed that birds' gizzards would respond to the two grit types in the same way and not retain one type longer than the other. We tested these assumptions experimentally. We gave 18 House Sparrows access for 14 days to a mixture of equal volumes of quartz and feldspar particles. Chi-square analysis of the contents of individual gizzards revealed that in 13 of the gizzards the number of particles of the two grit types did not differ significantly ($P > 0.05$). Four of the remaining five gizzards contained more quartz grit, and one contained more feldspar. In the Quartz-to-Feldspar and the Feldspar-to-Quartz Retention Experiments, we tested if birds would show the same pattern of grit replacement in gizzards when quartz was shifted to feldspar as when feldspar was shifted to quartz. The similarity in the results of these two experiments (see below) also supported the assumption that House Sparrows were unable to distinguish between quartz and feldspar particles. Although it is possible that the birds could detect differences between quartz and feldspar particles but showed no preference for either, we think this unlikely, given the difficulty we often had distinguishing between the two grit types under a stereomicroscope with optimal lighting (see below).

Before the experiments, which were conducted during November–January, the grit was hammermilled and then tumbled in a vibrating tumbler for five days to dull any sharp, jagged edges. It then was sieved and sorted into 0.2-mm size classes. In all experiments except the Grit Size Retention Experiment, we used equal volumes of grit in the 0.2–0.4, >0.4–0.6, >0.6–0.8, >0.8–1.0, >1.0–1.2, and >1.2–1.4 mm size classes. In the Grit Size Retention Experiment, one group of birds was given only small (0.2–0.4 mm) grit, and another group was given only large (1.0–1.4 mm) grit. In all experiments, each grit tray initially contained 25 cc of grit, to which 2 cc of grit were added daily to ensure a continuous *ad libitum* supply.

In the laboratory, all quartz and feldspar particles in each gizzard were identified and counted. Because the quartz and feldspar particles were so similar in appearance, they could be distinguished only by using a microscope. Feldspar particles had flat cleavage planes on portions of their surfaces, whereas the surfaces of quartz particles were irregular throughout. The appearance of the particles when viewed through a polarized light filter also aided in distinguishing the two grit types.

RESULTS

GRIT USE BY FREE-RANGING HOUSE SPARROWS

All but 1 of the 245 gizzards of free-ranging House Sparrows contained grit. Grit counts in individual gizzards varied greatly, ranging from 0 to 3,204, with a mean of 580.3 (±489.6 [SD]) and a median of 462. There were no two-way or three-way interactions among sex, season, and diet that affected grit counts ($P \geq 0.159$). (The unexpected absence of an interaction between season and diet resulted from House Sparrows' consuming seeds and insects during both seasons.) Males and females did not differ in their mean grit counts overall (t = 0.33, 243 df, P = 0.743) or during either season (insect: t = 0.37, 127 df, P = 0.710; no insect: t = 0.38, 114 df, P = 0.704). Gizzards of House Sparrows captured during the insect season contained more grit particles than those of birds captured in September-February (insect = 673.6 ± 553.7, n = 129; no insect = 476.6 ± 382.9, n = 116; t = 3.20, 243 df, P = 0.002). Gizzards containing >75% animal food had more grit than those containing >75% plant material (animal = 681.2 ± 541.9, n = 85; plant = 530.9 ± 455.7, n = 156; t = 2.29, 239 df, P = 0.023).

Grit particles in the 60 House Sparrow gizzards in which individual particles were analyzed ranged in size from 0.1 mm to 2.4 mm, with a mean of 0.5 mm (±0.1 [SD]). The most common grit size class was 0.3–0.4 mm (24% of all grit particles), and more than two-thirds of the grit in the 60 gizzards was between 0.2 and 0.5 mm. Mean grit size did not differ between the sexes (t = 0.60, 58 df, P = 0.548) or seasons (t = 0.84, 58 df, P = 0.407). Only 8 of the 60 gizzards for which individual grit particles were measured contained >75% animal food material. Therefore, meaningful comparisons between diets could not be made for grit size, shape, and surface texture.

Shape index values of grit particles in the 60 House Sparrow gizzards ranged from 1.0 (approximately spherical) to 7.2 (oblong), with a mean value of 2.0 ± 0.2. The distribution of grit particle shapes was highly skewed toward more spherical shapes; most (79%) particles had shape index values of less than 2.0. Mean grit shape index values did not differ between the sexes (t = 0.67, 58 df, P = 0.505). Grit in gizzards of House Sparrows captured during the insect season had lower mean shape index values than grit in birds captured at other times of year (insect = 1.9 ± 0.1, n = 29; no insect = 2.0 ± 0.2, n = 31; t = 2.16, 58 df, P = 0.035), although this difference was probably not biologically meaningful.

House Sparrow grit tended to be of intermediate surface textures, with more than half (54%) of all particles sampled being sub-rounded, and less than 5% being angular or well-rounded. Mean grit surface-texture values (3.0 ± 0.2 overall) did not differ between the sexes (t = 1.10, 58 df, P = 0.276) or between seasons (t = 0.91, 58 df, P = 0.368).

GRIT SIZE EXPERIMENT

Birds consuming small grit had more particles in their gizzards than birds consuming large grit (t = 3.46, 48 df, P = 0.001). The mean grit count among birds using small grit was more than five times that of birds using large grit (275.1 ± 322.3 vs. 51.4 ± 26.4; ranges: 10–1,191 vs. 16–114). Responses of males and females were similar (small grit: t = 0.50, 23 df, P = 0.621; large grit: t = 1.07, 23 df, P = 0.297).

The large differences in numbers of particles of the two grit sizes found in gizzards suggested that the birds consuming small grit had used more particles to satisfy a need for a specific volume of grit in the gizzard. We examined this by estimating mean grit volumes for birds in the two grit-size treatments. By counting the particles in 40 cc of large and 1 cc of small grit, we found that it took about 45 times as many small particles as large ones to occupy the same volume of space (1 cc). A mean volume per particle (including inter-particle spaces) was calculated for each grit size, and from these values we determined that birds consuming large grit had a mean grit volume more than eight times that of birds using small grit (0.09 ± 0.05 vs. 0.01 ± 0.01 cc).

DIET EXPERIMENT

Overall, mean numbers of grit particles in the gizzards of birds on the two diets did not differ (plant = 130.3 ± 206.2 [range 18–1,120]; animal = 112.8 ± 68.0 [11–322]; t = 0.39, 48 df, P = 0.696). Among females, however, gizzards of birds on the animal diet contained more grit particles than those of birds on the plant diet (animal = 143.0 ± 78.7; plant = 78.5 ± 46.3; t = 2.55, 24 df, P = 0.018).

Grit in gizzards of birds on the two diets did not differ in mean size (both = 0.8 mm ± 0.1; t = 0.60, 48 df, P = 0.552). There was no evident relationship between mean grit size and number of grit particles in gizzards of House Sparrows maintained on either diet (plant: n = 25, r = 0.497; animal: n = 25, r = 0.214).

GRIT RETENTION EXPERIMENTS

The results of the Quartz-to-Feldspar and Feldspar-to-Quartz Retention Experiments were very similar (Fig. 1A). In both experiments, replacement in gizzards of the initial grit type by the

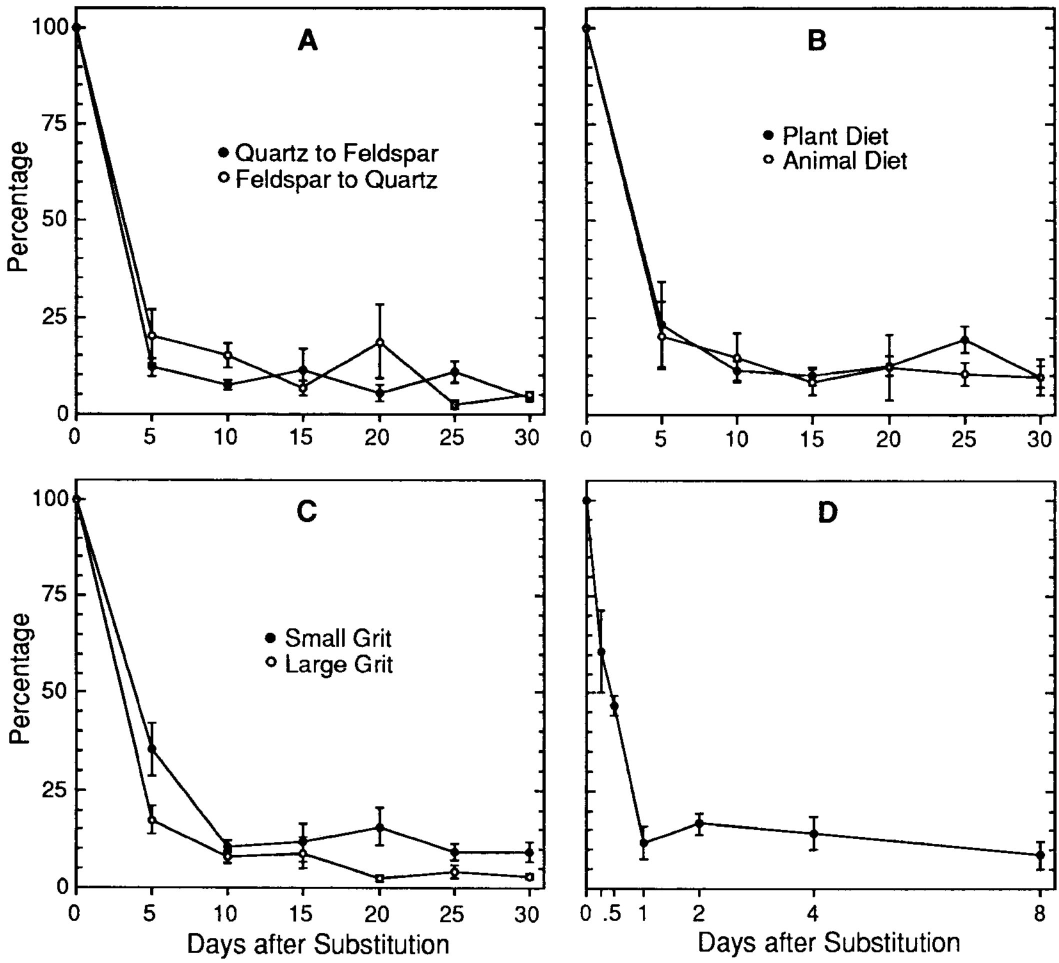

FIGURE 1. Grit Retention Experiments. Values represent percentages ($\bar{x} \pm$ SE) of the gizzard grit that were of the first grit type given, expressed as a function of the number of days after substituting the second grit type for the first. A. Quartz-to-Feldspar and Feldspar-to-Quartz Experiments. B. Diet Experiment. C. Grit Size Experiment. D. Short Intervals Experiment.

second type was very rapid during the first five days, followed by much more gradual replacement until the end of the experiment at 30 days. Mean numbers of grit particles per gizzard in these two experiments did not differ (Quartz-to-Feldspar: 257.3 ± 139.2; Feldspar-to-Quartz: 197.5 ± 137.5; $t = 1.67$, 58 df, $P = 0.100$).

In the Diet Retention Experiment, the temporal patterns of grit replacement in gizzards of birds were similar to those in the Quartz-to-Feldspar and Feldspar-to-Quartz Retention Experiments (Fig. 1B). Grit turnover did not differ between birds fed plant food and those fed animal material. Birds in the two groups differed, however, in the mean number of grit particles per gizzard (plant diet: 538.4 ± 330.6; animal diet: 205.1 ± 110.3; $t = 5.16$, 57 df, $P < 0.001$).

In the Grit Size Retention Experiment, House Sparrows given only small grit consistently retained grit longer than those given only large grit (Fig. 1C). In both grit size treatments, as in the other retention experiments, most of the grit in gizzards was replaced within five days. Gizzards of birds consuming small grit, however, contained comparatively large proportions ($\bar{x} = 35\%$) of quartz grit five days after the birds had been switched to feldspar grit (Fig. 1C). Corresponding mean values for birds in other retention experiments never exceeded 25% (Fig. 1A, B). In the Grit Size Retention Experiment, birds given small grit averaged nearly five times more grit particles per gizzard than those given large grit (853.0 ± 736.9 vs. 173.5 ± 90.7; $t = 5.01$, 58 df, $P < 0.001$). Seven of the 30 House Sparrows given small grit had more than 1,500 particles per gizzard, whereas the greatest number of large particles found in a single gizzard was 415. These results indicate that, when birds use small grit, their gizzards retain individual grit particles longer and contain more particles than when relatively large grit is consumed.

The Short Intervals Retention Experiment characterized grit retention and replacement during the critical first few days after substitution of feldspar for quartz. The results suggest that grit consumption, at least under the conditions of this experiment, is a daily activity (Fig. 1D). Moreover, much of the grit consumed by birds may be retained for only a few hours. Nearly 40% of the grit found in gizzards of experimental birds euthanized only 6 hr after the shift to feldspar grit was feldspar. Among birds euthanized 24 hr after grit substitution, a mean of only 12% of the grit in gizzards was quartz. The quartz proportion remained fairly stable throughout the remaining seven days of the experiment.

DISCUSSION

Free-ranging House Sparrows in central Iowa use large amounts of grit throughout the year. This finding is consistent with the results of German research, which showed that year-round, by weight, House Sparrow gizzards contained 66% grit and 34% food (Pfeifer and Keil 1962, cited in Keil 1973). Analysis of additional German House Sparrow gizzards collected in winter yielded similar results (65% grit and 35% food) (Keil 1973). In Poland, only one of 1,337 female House Sparrow gizzards collected during the breeding season lacked grit, and grit weight consistently exceeded food weight (Pinowska 1975).

Free-ranging House Sparrow males and females did not differ in the numbers of grit particles in their gizzards nor in the mean values for grit size, shape, and surface texture. Differences in grit use between the sexes are not always evident (Siegfried 1973; Alonso 1985; Norman and Brown 1985; Gionfriddo and Best, unpubl. data). When present, such differences may be related to increased calcium requirements of females during egg laying. Reproductive female birds are able to adjust their consumption of calcareous grit to meet the calcium demands of egg laying (Sadler 1961, Harper 1964, Taylor 1970). Pinowska and Kraśnicki (1985) found that female House Sparrows increased their grit use for about two days during egg laying to meet elevated calcium and magnesium requirements. Our study was not designed to detect grit-use shifts of such short duration.

Characteristics of grit used by free-ranging Iowa House Sparrows differed slightly from those reported for a sample of 77 midwestern House Sparrows (Best and Gionfriddo 1991). Grit in gizzards in the present study was smaller (mean size = 0.5 vs. 0.7 mm), more oblong (mean shape = 2.0 vs. 1.7), and less angular (mean surface texture = 3.0 vs. 2.8). Moreover, the median grit count per gizzard was 6 times greater than in the midwestern birds (462 vs. 69). These differences, however, may simply reflect the substantial variation in grit use observed among House Sparrows captured at different locations (Gionfriddo and Best, unpubl. data). Such variation probably is influenced by geographical differences in the availability of various types of grit. The differences in median grit counts between the two House Sparrow samples probably are related to the differences in mean grit size. Human error and subjectivity in making the measurements also could have contributed to the differences between the studies.

Grit size seems to be a major factor influencing grit use. Birds consuming small grit are likely to use more grit particles than those consuming larger grit. In both the Grit Size Experiment and the Grit Size Retention Experiment, gizzards of House Sparrows consuming small grit contained about five times as many particles as those of birds consuming large grit. These results are consistent with the pattern that we observed in free-ranging House Sparrows (see above) and with the findings of other researchers. Smith (1960) reported that voluntary grit consumption by domestic chicks (*Gallus domesticus*) declined significantly with increasing grit size. Several field studies also have determined that, in general, the larger the size of the grit particles, the fewer are ingested and retained in the gizzard (Myrberget et al. 1975, Norris et al. 1975, Alonso 1985). Free-ranging birds typically have access to and use a wide range of grit particle sizes (Best and Gionfriddo 1991).

Avian grit use also is influenced by diet. The ultimate (functional) cause of many grit-use shifts probably is seasonal dietary changes that produce variation in the value of grit. Field studies have documented seasonal diet and grit-use changes in several avian species. Hogstad (1988) reported that grit use by Bramblings (*Fringilla montifringilla*) was much greater when they consumed seeds than when they shifted to soft insect larvae. As Dunnocks (*Prunella modularis*) changed their diet in late summer from insects to seeds and insects, their grit use increased significantly (Bishton 1986). A similar association between increased grit use and greater consumption of hard (usually plant) foods also has been documented in other research (Meinertzhagen 1954, Porkert 1972, Norris et al. 1975) and in our Diet Retention Experiment.

In House Sparrows, the efficient digestion of hard-bodied coleopterans (which constitute more than half the animal matter consumed [Kalmbach 1940, Gavett and Wakeley 1986]) may require an increase in grit use. Pinowska (1975) reported that grit weight increased and decreased with the frequency of insects in gizzards of female House Sparrows during the breeding season and concluded that grit may assist in the digestion of chitinous insect parts. Free-ranging birds in Iowa (present study) used more grit when they fed heavily on insects (>75% of the food in the gizzard) than when they consumed primarily seeds. Their gizzards also contained more grit during the months when insects were consumed relatively heavily (March and August) than during the months when they were not (September–February).

The identity of the proximate cue (e.g., dietary or photoperiod change) that triggers seasonal changes in avian grit use remains uncertain. Some evidence suggests that such grit-use shifts may be elicited by changes in diet. Experiments with captive Willow Ptarmigan (*Lagopus lagopus*) showed that birds consuming coarse food (twigs and buds of willow [*Salix*] and birch [*Betula*]) ingested and excreted 2–4 times as much grit as birds fed pelleted food, and that ptarmigan kept on a constant diet maintained a constant grit intake throughout the year (Norris et al. 1975). Other evidence, however, is equivocal. For example, two of our experiments with captive House Sparrows simultaneously compared grit use by birds on two diets (hard plant and soft animal). In the Diet Retention Experiment, gizzards of birds consuming plant food had more than twice as much grit as those of birds fed Hill's dog food. In the Diet Experiment, however, although more grit was found in gizzards of birds fed plant food than in those of birds fed Ken-L-Ration dog food, the difference was not significant statistically. Why the birds consuming Ken-L-Ration in the Diet Experiment used about as much grit as birds fed seeds is uncertain, but may be related to the amount of roughage in the dog food. Ken-L-Ration contains three times more crude fiber than Hill's dog food (according to labels). The latter is specially formulated for high digestibility and thus better represents a "soft animal food."

Although we found no evidence of seasonal changes in House Sparrow grit size, such changes have been documented in other avian species with seasonal diet shifts. May and Braun (1973) found that White-tailed Ptarmigan (*Lagopus leucurus*) used proportionately more large grit during seasons when hard, difficult-to-digest food items (willow buds, twigs, and leaves) were consumed. Alonso (1985) reported that Spanish Sparrows (*Passer hispaniolensis*) consumed larger grit particles when they fed on large insects and cereal grains (spring and summer) than when they fed mainly on seeds (fall and winter). He concluded that food item size (rather than hardness) determined the size of grit particles used. Because grit facilitates the mechanical breakdown of food in the gizzard, it is likely that grit use by many avian species is influenced by the sizes and types of food consumed.

The retention of individual grit particles in birds' gizzards is highly variable. Under certain conditions, such as when birds are denied access to grit, retention may be very long, even >1 year (Kraupp 1924, Walter and Aitken 1961, Robel and Bisset 1979). On the other hand, when birds have daily access to abundant grit sources, they may continually replenish grit in their gizzards (Lienhart 1953, May and Braun 1973, Alonso 1985). In the latter instance, many grit particles may be retained only briefly in the gizzard, passing completely through the digestive tract in a few hours. Why other particles are retained in the gizzard for relatively long periods is unknown, but grit characteristics such as size, shape, and surface texture may play a role. Of the variables examined in our research, grit particle size seemed to exert the most influence on retention. In general, smaller grit particles were retained longer than larger particles when birds were given either small or large grit. This result, however, differs from the findings of other laboratory studies in which groups of domestic chicks were fed (*ad libitum*) grit of different sizes (one size per group). Smith (1960) found that grit retention on a percentage ingested basis increased with increasing grit size. Tagami (1974), on the other hand, reported that chicks retained more medium-sized (1.2–2.4 mm) than large (2.4–3.4 mm) particles, and very few small (0.6–1.2 mm) particles. Gizzards of free-ranging birds, however, usually contain grit particles of many different sizes (Best and Gionfriddo 1991), and in nature, retention processes act on grit particles representing a much wider range of sizes than those in gizzards of these experimental birds.

The results of our research have implications relative to avian exposure to granular pesticides because one potential route of exposure involves birds' mistakenly consuming granules as a source of grit (Best and Fischer 1992). Granular pesticides are applied during the spring and summer, when free-ranging birds generally have access to abundant sources of grit. Under such conditions, lengthy retention of grit in gizzards is not necessary because the grit in gizzards can be replenished daily. As a result, birds may face a greater risk of exposure to pesticide granules by consuming grit often. Furthermore, at least in some avian species, grit use increases during this time of year. Documenting seasonal and other patterns in grit use by birds, as we have done with House Sparrows, will improve our knowledge of the relative vulnerabilities of various groups of birds to granular pesticide use. If ingestion of pesticide granules is an important route of avian exposure, then an understanding of the grit-use preferences (grit size, shape, surface texture, etc.) and patterns (seasonal, sexual, dietary, etc.) of other species may be useful in designing pesticide granules to make them less attractive to birds.

House Sparrow behavior in the artificial conditions of the aviary may not accurately represent the behavior of free-ranging birds in a natural environment. Grit consumption rates of captive birds may have been abnormally high or low. For example, captivity-induced "boredom" may have led to abnormally high grit consumption rates. If that occurred, then the high turnover rates (short retention) of grit in gizzards of the captive birds could simply have resulted from artificially accelerated grit consumption. High grit turnover rates, however, also were found in free-ranging House Sparrows (Fischer and Best, in press). Also, the fact that the mean grit counts in gizzards of free-ranging House Sparrows in the present study were greater than those of experimental birds suggests that the grit consumption rates of the captive birds were not abnormally high. The relatively low grit counts in the experimental birds may have been related to the birds' responses to the surfaces (bottoms) of the grit trays. In the Diet and Grit Size Experiments, the slippery texture of the Masonite® used as grit tray bottoms may have made birds uncomfortable, reducing the time they spent in the grit trays. Mean grit counts per gizzard were greater when the concrete aviary floor was used as grit tray bottoms (in the Grit Retention Experiments), and greater still when a crusted soil surface was used (Gionfriddo and Best, unpubl. data). Although our study has limitations, it represents one of the first experimental attempts to quantify the influences of grit size and bird diet on grit use and on the retention and replacement of grit in the gizzard. As such, it constitutes an important first step in understanding the dynamics of grit use and retention in birds.

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