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THE ROLE OF GASTROLITES ON FEEDING BEHAVIOR AND DIGESTIVE EFFICIENCY IN THE RUFOUS-COLLARED SPARROW[1]

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Abstract. We examined grit consumption in the facultative granivorous Rufous-collared Sparrow (*Zonotrichia capensis*). Grit consumption fluctuated seasonally and was significantly correlated with morphological changes in the digestive tract, and with seed size. The highest values of grit consumption and digestive tract mass were observed during winter. Laboratory experiments suggested that grit consumption was a voluntary behavior rather than the result of accidental ingestion, and favored digestibility. Grit consumption varied considerably when *Z. capensis* fed on different types of food, but remained constant when food availability varied. We suggest that grit consumption together with morphological changes in the digestive tract allow *Z. capensis* to increase energy acquisition in response to higher energy demands during wintertime.

Key words: assimilation efficiency, digestive tract morphology, grit consumption, Rufous-collared Sparrow, Zonotrichia capensis.

In granivorous birds, variables such as seed size and

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hardness may influence foraging and digestion (Karasov 1996). Granivorous birds can increase digestive efficiency by grit ingestion and changes in the mass of the gizzard (López-Calleja 1995, Novoa et al. 1996). In fact, the presence of gastrolites, such as shells and grit, may be an important agent for enhancing digestibility by grinding food in the gizzard (Alonso 1985, Duke 1986, Piersma et al. 1993). On the other hand, Gionfriddo (1995) found that House Sparrows (*Passer domesticus*) consumed different amounts of grit depending on the size of the grit. However, comparatively few studies associate behavioral and physiological features with grit ingestion.

To understand the role of grit on diet selection and digestive efficiency, we examined grit use by the Rufous-collared Sparrow (*Zonotrichia capensis*) under field and laboratory conditions. *Zonotrichia capensis* is a widespread granivore that consumes mainly seeds, but also includes insects in its diet (López-Calleja 1995). The presence of gastrolites in the gut of *Z. capensis* enabled us to examine several aspects related to grit ingestion. Field observations allowed us to evaluate the relationships between grit consumption, digestive physiology, and some environmental features, such as temperature and photoperiod, as well as the effects of sex, age, and seasonal changes. Laboratory experiments allowed us to determine whether grit consumption occurs voluntarily and to evaluate anatomical changes of the digestive tract and changes in digestive efficiency related to grit ingestion and grit availability.

METHODS

STUDY SITE

Zonotrichia capensis were collected bimonthly during 1991–1992 at El Pangue (central Chile; 33°17′S, 71°11′W). This area has a typical Mediterranean environment, with warm, dry summers and cool, moist winters. The rainy season occurs from June to September, with an average of 500 mm of annual precipitation. There is also marked seasonal variation in seeds and insects (Atkins 1977, Montenegro et al. 1978). Each individual was sexed and weighed, and digestive tracts were preserved in 70% alcohol for dietary analysis.

Diet characterization was carried out in the laboratory by direct observation of gut contents with a binocular magnifying glass (20×). Vegetable, animal, and mineral contents were separated, weighed, and quantified. Fresh length (± 0.1 mm) and dry mass (± 0.1 mg) of gizzard, small intestine, and large intestine were determined following Bozinovic et al. (1990). Values were standardized by body mass (Karasov 1990).

ANIMAL MAINTENANCE IN THE LABORATORY

For laboratory experiments, animals were captured at the same field locality with mist nests from June to November 1996, and maintained in individual cages (0.4 × 0.3 × 0.3 m) under a 12D:12L photoperiod and a mean temperature of 20 ± 1°C. For 30 days of captivity, birds were provided with the same food they later received during experiments (below). We chose three food types: birdseed (*Phalaris sp.*, small and soft), hemp (*Cannabis sp.*, large and hard), and mealworm (larvae of *Tenebrio molitor*). These three food types varied in physical properties such as size and hardness. Birds were provided with water, a range of food and grit ad libitum, depending on the experiment. Grit supplied was sifted to yield a size range from 0.8 to 1.2 mm.

BEHAVIORAL EXPERIMENTS

To determine the effects of food type on grit consumption, birds ($n = 20$) were maintained in individual cages (0.5 × 0.5 × 0.5 m) for 5 days. Cages were separated into two identical compartments in which birds had free access to both compartments. Grit and food were offered separately, one item per compartment. The experiment was repeated with the three food types, using different individuals in each series. After a period of 24 hr, food was weighed and stored, after drying it at 60°C to constant weight. After the experiment, we determined food and grit intake gravimetrically.

A similar experiment was done to determine the effects of food availability on grit consumption. Birds were maintained in individual cages where we offered food (birdseed) mixed with grit. Food/grit ratio was manipulated from 20% to 80% of seeds (5 series of food/grit ratio: 20/80, 40/60, 50/50, 60/40, and 80/20). Each proportion was maintained for 3 days, after which the seed/grit ratio was randomly changed.

PHYSIOLOGICAL EXPERIMENTS

To determine the effects of grit ingestion on digestive efficiency and morphological features, two groups of birds were acclimated for 15 days to the same diet they later received during experiments. Only one group had access to grit, while the other had access only to food. After the 15-day acclimation period, we conducted feeding trials for 3 days, offering each bird a weighed amount (10 g) of commercial birdseed and collecting its excreta and food remains. Both excreta and food remains were weighed and stored, after drying them. Apparent digestibility was calculated as $[(Q_i - Q_e)/Q_i] \times 100\%$, where Q_i = daily weight of dry matter consumption and Q_e = daily weight of dry excreta production. Food and excreta were burned, and ash weight was eliminated from dry matter values to estimate Q_i and Q_e, avoiding the error ensuing from grit contents in excreta. Digestibility is apparent because this method incorporates the contribution of metabolic and urinary wastes, and nonreabsorbed secretions of the digestive system, underestimating digestive efficiency (Karasov 1990). Animals were sacrificed immediately after the experiment and digestive tracts were removed and washed with physiological saline. Determination of dry mass (DM) of the organs was performed as described above. Fresh length of the digestive tract was determined and values were standardized by body mass$^{0.33}$ (Karasov 1990).

STATISTICAL ANALYSES

For field data, a one-way ANOVA was applied in seasonal comparisons, followed by an *a posteriori* Tukey test. Pearson correlation was used to analyze the relation between grit, food, and variation in organ size.

To analyze laboratory results, the effect of food type on grit consumption was assessed with a one-way ANOVA by ranks, using the *a posteriori* Tukey test for multiple comparisons between groups (Zar 1996). Repeated-measures ANOVA by ranks was used to determine the significance of the effect of food availability on grit consumption. Finally, comparisons between two independent samples were conducted with two-tailed *t*-tests, and body mass changes were analyzed with a Wilcoxon matched pairs test. In all cases, significance level was 5%, with results reported as mean ± SD.

RESULTS

DIETARY AND DIGESTIVE CHARACTERIZATION

We collected 94 birds during 1991 and 1992, with a mean body mass of 22.2 ± 1.4 g that showed no significant variation over this period ($F_{5,88}$ = 1.5, P = 0.20). All individuals had grit in their gizzards. The number of grit particles per gizzard ranged from 4 to 1,682 (mean of 280.6 ± 307.7). Mean mass of grit per gizzard (W_{grit}) was 114.8 ± 77.0 mg, ranging from 7.0 to 430.7 mg. Grit content was mostly quartz and granite particles, typical topsoil components of the study area (Rovira 1983). To determine the preferred grit size, we first discarded the microgranular fraction (< 0.1 mm), because it likely consisted of remains of larger particles. Grit size ranged from 0.1 to 3.2 mm, and grit measuring 0.4 to 0.8 mm accounted for 42% of the whole sample.

A total of 31 females and 43 males was captured during the two years, and no relation between W_{grit} and sex was found ($F_{1,72}$ = 0.4, P = 0.54). Five juveniles were captured in January 1991, and comparison between them and seven adults captured during the same period did not show any significant difference on grit consumption (ANOVA by ranks, $F_{1,10}$ = 0.3, P = 0.61).

DIETARY EFFECTS ON GRIT CONSUMPTION

Both grit and food weight showed significant seasonal fluctuations (Table 1). Grit mass per gizzard was significantly higher during autumn and winter. On the other hand, there were significant differences in the gizzard contents through the year, with a clear increase during the same period mentioned above (March–July), reaching a maximum value in July. The diet of *Z. capensis* showed a high prevalence of seeds, followed by insects. The number of these trophic items did not show any significant trend during the year (Table 1). However, the mean weight of seeds (MSW), calculated as the ratio between seed mass and total number of seeds found in the gizzard, was seasonally variable, reaching its highest value during July (Fig. 1). In addition, fluctuations in W_{grit} showed a positive significant correlation with MSW (r = 0.42, P < 0.001; Fig. 2).

GRIT INGESTION AND DIGESTIVE MORPHOLOGY

Seasonal variations were detected in both gizzard and small intestine weight (Fig. 1), particularly during autumn and winter. We found a significant positive correlation between grit consumption and both gizzard and small intestine mass (r = 0.63, P < 0.001; r = 0.29, P < 0.001, respectively).

TABLE 1. Field data on gizzard contents, and diet characterization of *Z. capensis*. *P*-values were obtained with a one-way ANOVA. Values showing the same letter across months are not significantly different according to *a posteriori* Tukey tests. Values are shown as mean ± SD of data obtained in 2 years of observations.

	January	March	May	July	September	November	*P*
N	20	16	15	11	13	19	
Gizzard content (mg)							
Total	151.0 ± 51.9A,D	210.2 ± 40.6A,B	261.6 ± 89.9B,C	301.6 ± 83.0C	157.7 ± 107.8A,D	117.9 ± 50.2D	<0.001
Seed and insect	68.1 ± 30.3A,C	94.9 ± 36.1A,B	83.6 ± 45.2A,B	128.5 ± 65.5B	39.2 ± 33.0C	51.2 ± 35.7A,C	<0.001
Grit (%)	54.8 ± 19.3A	50.9 ± 12.7A	66.0 ± 17.2A,B	55.4 ± 22.2A,B	76.3 ± 18.9B	58.6 ± 21.8A,B	<0.01
Diet (No. items)							
Insects	7.3 ± 9.8	4.9 ± 9.0	5.6 ± 5.8	3.7 ± 3.3	5.1 ± 4.2	8.5 ± 11.3	0.78
Seeds	81.4 ± 104.8	63.5 ± 41.0	34.5 ± 26.9	65.8 ± 94.7	23.9 ± 27.1	70.3 ± 123.9	0.37

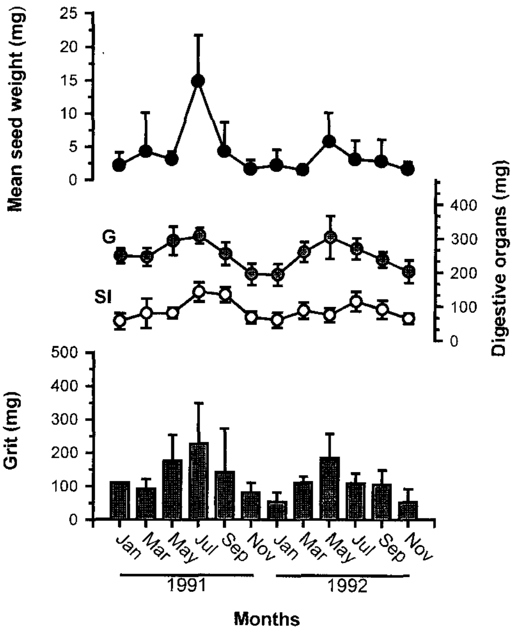

FIGURE 1. Seasonal fluctuations in grit consumption, gizzard (G) and small intestine mass (SI), and mean weight of seeds consumed (MSW). Grit consumption is significantly correlated with the other three features, according to a Pearson correlation analysis. Values are shown as mean ± SD.

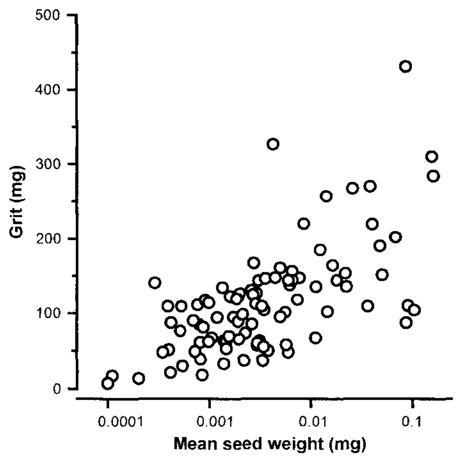

FIGURE 2. Correlation between grit weight and mean seed weight (MSW). These variables are significantly correlated according to a Pearson correlation analysis.

BEHAVIORAL EXPERIMENTS

Grit consumption varied significantly when we offered different types of food (Table 2). The *a posteriori* Tukey test revealed that grit consumption decreased significantly in treatments with insect larvae. Body mass increase during the experiments was significant only in birds fed mealworms (Wilcoxon, $Z = 2.2$, $P = 0.03$; Table 2).

No effect on grit consumption was found when *Z. capensis* was faced with different seed/grit ratios (repeated-measures ANOVA, $F_{4,16} = 1.6$, $P = 0.21$). Birds maintained a constant rate of grit consumption, with a mean value of 0.16 ± 0.07 g, being similar to the values obtained in previous experiments with seeds (Table 2).

PHYSIOLOGICAL EXPERIMENTS

No significant differences were detected in length or dry mass of gizzard, small and large intestines associated with grit consumption. However, we found a digestibility of 76.8 ± 3.6% when there was no access to grit and 82.2 ± 2.8% in the other treatment. Therefore, grit ingestion led to a significant increment of 7% in digestibility ($t_9 = -2.9$, $P = 0.02$).

DISCUSSION

Grit consumption seems to be a common behavior in *Z. capensis*. All individuals studied had grit in their gizzard, and no significant differences were observed when we analyzed the effects of sex and age on dietary and digestive features.

Fluctuations in grit and food consumption seem to be coupled, as well as morphological changes in both gizzard and small intestine (Fig. 1). This coupling may depend on two factors: energetic demands, which could explain the increases in gizzard size and small intestine during autumn-winter (Dykstra and Karasov 1992), and diet. Because grit consumption is proportional to the mean weight of seeds (MSW), we postulate that seed size and hardness may be another feature accounting for the pattern described above.

Grit consumption decreased when *Z. capensis* was fed mealworms. Grit is probably not needed to process this soft, highly profitable food. This is consistent with the fact that *Z. capensis* had a positive body-mass balance only in the treatments where mealworms were available, whereas with other diets birds maintained

TABLE 2. Food and grit consumption by *Z. capensis* faced with different food types. Values represent mean ± SD. *P*-values obtained after a one-way ANOVA are shown. Value with different letters represent significant differences between groups after *a posteriori* Tukey tests.

	Birdseed	Hemp	Mealworms	*P*
Grit consumption (g day^{-1})	0.15 ± 0.07A	0.12 ± 0.05A	0.03 ± 0.03B	<0.01
Food consumption (g day^{-1})	3.27 ± 0.73A	2.48 ± 0.32A	9.07 ± 1.85B	<0.001
Body mass change (g)	0.22 ± 0.57A,B	−1.58 ± 2.19A	1.06 ± 0.67B	<0.01

mass balance but could not increase body mass (Table 2). However, these results seem contradictory with field data, where no change in grit consumption was noticed. This pattern may be explained because birds maintained a mixed diet of seeds and insects in the field.

We suggest that grit use by *Z. capensis* is a voluntary behavior rather than the result of accidental ingestion. In the laboratory, these birds maintained a constant ingestion rate of grit in the face of changes in the availability of food resources, which means that they distinguished grit from food. Field studies have documented seasonal changes in diet and grit use among birds, and some have reported decreases in grit use associated with seasonal increments in larvae consumption (Bishton 1986, Hogstad 1988). This pattern was not detected in our study. However, we did observe fluctuations in grit consumption depending on energy demands and physical properties of food. Seasonal changes in digestive organ size, mass, and capacity have been described in other animals (Bozinovic 1993).

Mechanisms that may induce reductions in grit consumption remain unclear. Some studies suggest that physical properties such as hardness may be determinant in grit use (Norris et al. 1975, Gionfriddo and Best 1995). Our results support this hypothesis, because grit intake was significantly correlated with MSW (Fig. 2).

In summary, grit consumption is a complex, voluntary behavior related to both diet type and environmental characteristics. It may increase grinding effectiveness by accelerating mechanical processing of food, therefore increasing energy and nutrient acquisition. Its importance in digestive efficiency as well as its widespread use among birds led us to consider this mechanism in digestive models, a factor that has not been conceptually incorporated into these models.

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