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Variation between Sparrows in the Ability to Extract Buried Seed

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VARIATION BETWEEN SPARROWS IN ABILITY TO EXTRACT BURIED SEEDS

A Thesis
Presented to
The Faculty of the Department of Biology
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

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by
David M. Whalen
1998

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Arts

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DEDICATION

This work is dedicated to my parents, Thomas and Kathryn Whalen, who have always encouraged my intellectual and personal fulfillment through their unfailing support and affection.

TABLE OF CONTENTS

Page

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LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

ABSTRACT

Most North American sparrows forage almost exclusively on herbaceous seeds during the winter months. Limited amounts of surface seed force some birds to employ a bilateral scratching behavior to extract seeds buried beneath soil, snow, or litter. Artificial seed trays were used to test the ability of six different sparrow species to extract seed buried at different depths in soil. The results suggest three functional groups based on relative scratching ability. Strong scratchers, which included Eastern Towhee and Song and White-throated sparrows, met or exceeded their energetic requirements when foraging on seed buried at all depths (down to a maximum depth of 1.50-2.25 cm). A weak scratching species, Savannah Sparrow, scratched with the same frequency as the strong scratchers, but experienced negative energy budgets when forced to forage on sub-surface seed. Non-scratchers, which included Field Sparrow and Northern Cardinal, failed to secure any buried seed.

Level of scratching ability may impact foraging efficiency in habitats with low surface seed. As a result, interspecific differences in scratching ability may promote habitat selection. Strong scratchers may be adapted to foraging near woody vegetation where intense resource competition and abundant litter limit the availability of surface seed. Weak scratchers, on the other hand, may be forced to feed away from areas with little available surface seed. Since woody vegetation serves as a primary source of cover in early successional habitats, a tradeoff between foraging efficiency and the risk of predation may permit the local coexistence of species that differ in relative scratching ability and adaptations to evading predators.

VARIATION BETWEEN SPARROWS IN ABILITY TO EXTRACT BURIED SEEDS

INTRODUCTION

Seeds represent essential food resources for many granivorous organisms during the winter months, yet many seeds may be buried in soil, snow, or detritus (e.g., leaf litter). As a result, access to such resources may be limited. Some ground-foraging bird species, primarily New World sparrows (subfamily Emberizinae), use a bilateral scratching behavior to extract buried seed (Harrison 1967, Greenlaw 1977).

Birds initiate a bilateral scratch with a short forward hop that positions the feet close together and slightly in front of the main axis of the body. This forward hop is followed by a backward hop during which the feet are swept rapidly beneath the body while penetrating the foraging substrate. Birds may perform multiple scratches in rapid succession followed by pauses to inspect the substrate for available food items.

The ability of scratching birds to create sizable pits or depressions demonstrates their potential to access seed buried in soil. Some foraging Spotted Towhees (*Pipilo maculatus*), for example, produced depressions averaging 3.5 cm deep (Davis 1957). In addition to extracting seed buried in soil, birds may also scratch to access seed covered by litter. Although birds scratch in many different types of litter, prime examples include light, fibrous grass-forb (i.e., herbaceous) litter associated with grasslands as well as heavy broad-leaved litter associated with woodland edges and interiors (Greenlaw 1977). Sparrows that inhabit shrub and woodland edge habitats scratch grass-forb litter fairly regularly and may scratch broad-leaved litter as well (Greenlaw 1977). Grassland specialists, on the other hand, may scratch herbaceous litter, but evidence of these species scratching broad-leaved litter is generally lacking (Greenlaw 1977).

As a method of seed acquisition, scratching is a relatively plastic behavior. Both spatial and temporal variation exists in the use of scratching by sparrows. Birds capable of scratching appear to do so more during the non-breeding season when food becomes less abundant and seeds comprise the bulk of their diet (Greenlaw 1976). Likewise, at the patch-level, birds scratch in longer bouts when seeds become scarce (Burtt and Hailman 1979) and where litter layer is heavier (Hailman 1984). The value of scratching may be especially high during times of food scarcity. In patches or habitats where surface seed availability is low, species that are better adapted for scratching may enjoy a competitive advantage to less-efficient or non-scratching species.

The availability of certain food resources may vary between species with different foraging efficiencies. Several studies have addressed seed handling efficiencies in finches (Pulliam 1980, 1985, Schluter 1982). However, little is known about interspecific differences in how sparrow species may access seeds during the winter months. Although scratching is an important mode of seed acquisition used by the majority of North American sparrows (Greenlaw 1977), the use of this foraging method has been largely overlooked within the context of sparrow community studies. The primary objectives of this study are (1) to determine if interspecific variation exists in scratching ability within an assemblage of wintering sparrows, (2) to investigate whether individual species are able to access seed buried at varying depths with enough efficiency to meet their energetic requirements, (3) to make direct comparisons between the scratching efficiencies of two locally coexisting species, Savannah and Song sparrows, and (4) to extend these results to theoretical issues of habitat selection between coexisting sparrows in general.

STUDY SPECIES

Birds used in this study were New World finches belonging to the subfamily Emberizinae and included the following species: Savannah Sparrow (*Passerculus sandwichensis*), Field Sparrow (*Spizella pusilla*), Song Sparrow (*Melospiza melodia*), White-throated Sparrow (*Zonotrichia albicollis*), Eastern Towhee (*Pipilo erythrophthalmus*), and Northern Cardinal (*Cardinalis cardinalis*). Field Sparrow was the smallest species included in this study, Savannah, Song, and White-throated sparrows were intermediate in body mass, and Northern Cardinal and Eastern Towhee were heavier than the other species (Table 1).

All of these birds are fairly common winter residents throughout the Southeastern United States. During the winter months, these species become almost exclusively granivorous (Bent 1968), feeding primarily on grass and forb seeds (Pulliam and Enders 1971, Pulliam and Mills 1977).

Although many of the species included in this study may be found coexisting in the same habitats, species-specific habitat preferences can be arranged along a successional gradient. The utility of scratching behavior may increase along this gradient because, as old field succession progresses, the abundance of woody vegetation and litter increase while the amount of

Table 1. Mean body mass of each species.

Species	*N*	Mean Body Mass (g)	Standard Error (±)
Savannah Sparrow	4	19.4	0.56
Song Sparrow	4	22.1	1.05
White-throated Sparrow	4	22.8	0.75
Eastern Towhee [a]	4	38.5	1.62
Field Sparrow	4	13.1	0.52
Northern Cardinal [a]	4	36.4	1.71

[a] Eastern Towhees and Northern Cardinals each included 2 males and 2 females. The other species are not sexually dimorphic, therefore sexes were unknown.

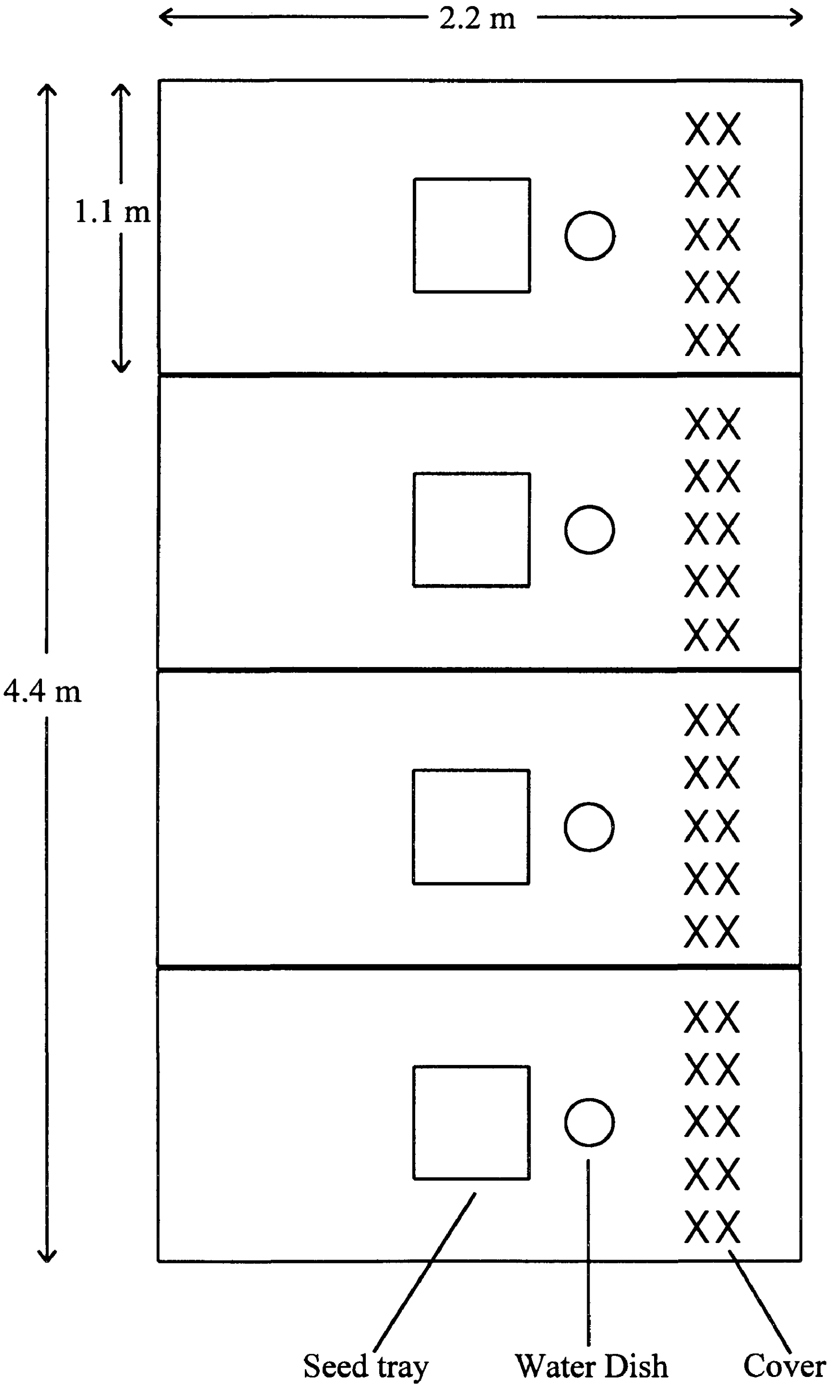
herbaceous growth and open space decline (Odum 1960). Savannah Sparrows occupy a variety of early successional habitats including open grassland interiors and field edges (Wheelwright and Rising 1993, Rising 1996). Field and Song sparrows occur near field edges and in old fields with scattered brush (Carey et al. 1994, Rising 1996). White-throated Sparrows use habitats with thick cover such as old fields and woodland edges (Falls and Kopachena 1994). Eastern Towhees are associated with woodland edges and old field thickets with dense woody cover and a well-developed litter layer (Greenlaw 1996). Finally, Northern Cardinals are found near woodland edges, in dense thickets, or in open woodland interiors (Rising 1996).

METHODS

Twenty four birds (four individuals of each species) were trapped in the vicinity of Williamsburg, VA in March and April of 1997. Birds were trapped with mist nets or potter traps baited with seed. Only birds that carried minimal fat loads at the time of capture were retained. Birds were housed in an indoor aviary at the College Landing Biological Laboratory (formerly called the Laboratory of Endocrinology and Population Ecology) at the College of William and Mary in Williamsburg. Birds were placed in individual rooms (i.e., one bird per room) which measured 2.2 x 1.1 x 2.4 m (Figure 1). Dividing walls between rooms prevented birds from seeing one another for the duration of the study. Each room contained vegetative cover in the form of Privet (*Ligustrum* sp.) and Red Cedar (*Juniperus virginiana*) branches. Water was provided *ad libitum* for the duration of the study and facilities were maintained on a natural photoperiod (i.e., approximately 12:12 h light:dark in March and April). To allow acclimation to the experimental facilities, birds were provided with seed *ad libitum* and were left undisturbed for two days prior to the first treatment.

Figure 1. Diagram of experimental facilities. Birds were housed individually (i.e., one bird per room) for the duration of the study. Cover consisted of Privet and Red Cedar branches.

DIAGRAM OF EXPERIMENTAL FACILITIES



Four experimental treatments were performed on each bird in this study. Wooden seed trays (measuring 32 x 31 x 4 cm) were used to test the ability of individual birds to extract seed from soil. Seed trays contained 2.25 L of sifted top soil and 2.00 g of white millet seed. Three layers, each containing 750 mL of soil, were evenly applied to each seed tray. The soil was then manually compacted with a small section of plywood. Each compacted soil layer was approximately 0.75 cm deep. Hence, the total depth of soil in each seed tray was about 2.25 cm. Treatments varied in the depth at which seed was located in the soil (Table 2). During Treatment 1, seed was spread evenly on the surface of the soil. For Treatments 2 - 4, seed was thoroughly mixed with 750 mL of soil which was then applied as one of the aforementioned soil layers in the seed tray. Only the top layer of soil contained seed during Treatment 2. The middle and bottom layers of soil contained seed during Treatments 3 and 4, respectively. In order to initiate feeding and to ensure that birds associated seed with the seed trays, 4 millet seeds (approximately 0.02 g) were placed on the surface of all seed trays before each treatment.

At dusk on the evening prior to each treatment, prepared seed trays were placed in the center of each room and then lights were turned off to prevent birds from consuming any seed at night. Treatments were initiated at dawn simply by turning on the lights. Birds commenced feeding within 5 min of the start of each treatment during 95 out of 96 trials. All rooms were

Table 2. Location of seed in the soil in each experimental treatment.

Treatment	Location of Seed	Mass of Seed (g)	Total Volume of Soil (L)	Total Depth of Soil (cm)
1	Soil Surface	2.00	2.25	2.25
2	Top Layer of Soil (0.00-0.75 cm depth)	2.00	2.25	2.25
3	Middle Layer of Soil (0.75-1.50 cm depth)	2.00	2.25	2.25
4	Bottom Layer of Soil (1.50-2.25 cm depth)	2.00	2.25	2.25

equipped with mounted video cameras which were used to videotape all experimental treatments for later analysis. Each treatment lasted 90 min. At the end of each treatment seed trays were collected and the soil was sifted to recover all remaining seeds. These seeds were then weighed to determine the quantity of seed consumed during the course of the treatment. Videotaped treatments were later analyzed to quantify the amount of time invested in foraging and the amount of scratching activity per treatment. Birds were considered to be foraging if they were standing in the seed tray and conducting one of the following activities: pecking at the soil, handling seeds, or scratching the soil. Birds standing in the seed tray but not conducting one of those three activities (e.g., birds that were preening) were not considered to be foraging.

Treatments were conducted in chronological order on four consecutive days (i.e., one treatment per day) for each bird in this study. Thus, seed was located at greater depths in the soil with each successive treatment. This design best mimics a hypothetical non-renewable food patch in which seed resources are initially distributed evenly across four layers in a vertical section of soil. Repeated-measures analysis of variance (ANOVA) was used for analyses across treatments. Since treatment order was not varied during this study, its effect is unknown. However, any biases resulting from treatment order should be conservative because seed became progressively more difficult to access with each successive treatment. Therefore, any possible effects of repeated testing (e.g., learning) should only cause species to become better at accessing seeds. All treatment effects presented in this study occurred in the opposite direction of any potential treatment order effects.

Repeated-measures ANOVA tests were performed on the following variables with species as the between-groups factor and treatment as the within-subjects factor: total seed consumption (measured to the nearest 0.01 g), body mass-specific seed consumption (g seed/g body mass), foraging time (measured the nearest sec), rate of seed consumption (g seed/min of foraging time), total number of scratches (log-transformed to normality), and seed consumption per scratch (mg seed/scratch). When ANOVA indicated significant trends across species, Tukey's Honestly Significant Difference tests were used for post-hoc comparisons between group means. Due to the nature of the treatments, seed could be consumed without scratching during Treatments 1 and 2, therefore these two treatments were excluded from analyses of scratching behavior (i.e., analyses involving total number of scratches and seed consumption per scratch). Scratching behavior was required for birds to procure seed during Treatments 3 and 4. Since Field Sparrows and Northern Cardinals do not scratch, they failed to respond to Treatments 3 and 4. Therefore, these two species were excluded from all analyses unless otherwise noted. In addition, one Song Sparrow failed to feed during the first treatment, therefore this individual was omitted from all analyses that included Treatment 1.

Savannah and Song sparrows represent the two most similar species in the present study in terms of body size, bill size (Pulliam and Enders 1971, Pulliam 1975), and plumage. Previous work has addressed differences in microhabitat use relative to cover between these two species (Watts 1990). These differences may impact foraging strategies used by each of these species. To allow more direct comparisons between the scratching abilities of these species, *t*-tests for independent samples were used for pairwise comparisons between Savannah and Song sparrows for each treatment in the present study.

Foraging performances were also analyzed from an energetic perspective. Estimates of field metabolic rates (FMR) were based on the following equation for passerine birds determined from a sample of numerous species under a wide range of field conditions (Nagy 1987):

$$\log y = 0.949 + 0.749 \log x$$

where y is metabolic rate in kJ/d and x is body weight in g. Estimates of FMR were calculated for individual birds based on the measured body mass of each individual (Table 3). Estimates of the mass of white millet seed required per day to maintain FMR were obtained by dividing FMR by the product of GE and MEC, where GE is gross energy content per gram of dry matter in kJ/g and MEC is the metabolizable energy coefficient (i.e., attainable proportion of food energy) (Karasov 1990). GE for white millet seed is 18.8 kJ/g (Saunders and Parrish 1987) and MEC for passerines feeding on a diet of cultivated seed

Table 3. Estimated field metabolic rates (FMR) and seed requirements of each individual bird.

Individual [a]	Body mass (g)	FMR (kJ/d)	Daily seed requirement (g)	Seed requirement per 90 min (g) [b]
SAVS-1	19.0	80.6	5.37	0.671
SAVS-2	21.0	87.0	5.78	0.723
SAVS-3	18.5	79.1	5.26	0.657
SAVS-4	19.0	80.7	5.37	0.671
SOSP-1	21.5	88.5	5.89	0.736
SOSP-2	20.0	83.8	5.58	0.697
SOSP-3	22.0	90.0	5.99	0.748
SOSP-4	25.0	99.1	6.59	0.824
WTSP-1	24.0	96.1	6.39	0.799
WTSP-2	22.0	90.0	5.99	0.748
WTSP-3	21.0	87.0	5.78	0.723
WTSP-4	24.0	96.1	6.39	0.799
EATO-1[c]	34.5	126	8.39	1.048
EATO-2[d]	40.0	141	9.37	1.171
EATO-3[c]	37.5	134	8.93	1.116
EATO-4[d]	42.0	146	9.72	1.215

Table 3. continued.

Individual [a]	Body mass (g)	FMR (kJ/d)	Daily seed requirement (g)	Seed requirement per 90 min (g) [b]
FISP-1	13.0	60.7	4.04	0.505
FISP-2	12.0	57.2	3.80	0.475
FISP-3	14.5	65.9	4.38	0.548
FISP-4	13.0	60.7	4.04	0.505
NOCA-1[c]	32.5	121	8.02	1.002
NOCA-2[c]	34.5	126	8.39	1.048
NOCA-3[d]	39.5	140	9.28	1.160
NOCA-4[d]	39.0	138	9.19	1.149

[a] SAVS = Savannah Sparrow, SOSP = Song Sparrow, WTSP = White-throated Sparrow, EATO = Eastern Towhee, FISP = Field Sparrow, NOCA = Northern Cardinal.

[b] Based on days with 12 h of daylight.

[c] females; [d] males.

has been determined to be 0.80 (Karasov 1990). Since all treatments were conducted in March and April, approximately 12 h of potential daily foraging time would be available. Thus, it was assumed that intake requirements for each 90 min treatment should be at least one-eighth of total daily requirements (Table 3).

Energy budgets were calculated for each individual bird by treatment combination as follows:

energy budget = (seed consumed - seed required) / seed required.

Thus an energy budget greater than zero (i.e., a positive energy budget) indicates that a bird exceeded its energetic requirements while an energy budget less than zero (i.e., a negative energy budget) indicates that a bird failed to meet its requirements.

Depending on scratching ability, seasonal variation in weather conditions during the winter could have different effects on the energy budgets of species feeding on buried seed. Passerines wintering in temperate regions cope with the heat loss associated with minimum winter temperatures by elevating metabolic rates (Pohl and West 1973, Dawson and Carey 1976, Dawson et al. 1983, Swanson 1991). Studies have suggested that maximum sustained FMR is limited to 3 - 5 times basal metabolic rate (BMR) (Drent and Daan 1980, Peterson et al. 1990, but see Bryant and Tatner 1991). Bioenergetic studies have shown that Savannah Sparrows consume more food at lower temperatures and that the FMR of individuals exposed to freezing temperatures is typically near 3.0 x BMR (Williams and Hansell 1981, Williams 1987). Therefore, 3.0 x BMR (with BMR calculated from Lasiewski and Dawson 1967) was used as a theoretical estimate of maximum sustained FMR in the present study. Estimates of maximum sustained FMR were calculated for Savannah and Song sparrows to determine the potential consequences of foraging on buried seed during times of maximum energetic stress (e.g., during minimum winter temperatures).

RESULTS

Foraging Performance

All Species

Table 4 provides a summary of all repeated-measures ANOVA's of foraging data. Significant differences were found among species in total seed consumption (Figure 2) and rate of seed consumption (Figure 3). The difference in total seed consumption resembled an allometric pattern proportional to body mass (seed consumption = -1.621 + 0.783 log (body mass), $r^2=0.88$, $P=0.064$). Although this pattern was marginally nonsignificant, a regression of seed consumption on log-transformed body mass in which each individual bird was considered an independent data point was highly significant (Figure 4; seed consumption = -1.590 + 0.776 log (body mass), $r^2=0.65$, $P<0.001$). As a result of this allometric relationship, body mass-specific seed consumption did not vary across species (Figure 5). Post-hoc comparisons (Tukey's tests) between species showed that the rate of seed consumption was significantly greater for Song Sparrows than for Savannah ($P=0.003$) and White-throated ($P=0.008$) sparrows. In addition, Song Sparrows consumed seed 1.5 times faster than larger-bodied Eastern Towhees but this difference was not significant ($P=0.115$).

Table 4. Results from repeated-measures ANOVA's on sparrow foraging data. [a,b,c]

				F statistics		
Dependent variable	Error MS	df Effect	df Error	Species	Treatment	Species x Treatment
Seed consumption	0.11	3	11	8.80**	---	---
	0.02	3	33	---	9.23***	---
	0.02	9	33	---	---	2.90*
Rate of seed consumption	<0.01	3	11	5.47*	---	---
	<0.01	3	33	---	34.68***	---
	<0.01	9	33	---	---	4.03**
Body mass-specific seed consumption	<0.01	3	11	2.03	---	---
	<0.01	3	33	---	8.66***	---
	<0.01	9	33	---	---	2.99*
Foraging time	0.10	3	11	3.03	---	---
	0.02	3	33	---	12.04***	---
	0.02	9	33	---	---	1.13

Table 4. continued.

Dependent variable	Error MS	df Effect	df Error	*F* statistics Species	 Treatment	 Species x Treatment
No. of scratches (Log transformed) [d]	0.23	3	12	1.19	---	---
	0.09	1	12	---	18.11***	---
	0.09	3	12	---	---	1.16
Seed consumption per scratch	0.04	3	12	8.20**	---	---
	0.03	1	12	---	37.70***	---
	0.03	3	12	---	---	0.42

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

[a] Species included in these analyses were Savannah, Song, and White-throated sparrows and Eastern Towhee.

[b] One Song Sparrow did not attempt to forage during Treatment 1, therefore this individual was omitted from all analyses that included Treatment 1.

[c] Scratching was not required during Treatments 1 and 2, therefore these two treatments were omitted from analyses of No. of scratches and Seed consumed per scratch.

[d] Log transformation was necessary to normalize this data.

Figure 2. Mean mass of seed consumed by each species during each 90 min treatment. Whiskers indicate ± SE. Treatments varied in the location (depth) of seed in the soil (see Table 2). SAVS=Savannah Sparrow; SOSP=Song Sparrow; WTSP=White-throated Sparrow; EATO=Eastern Towhee.

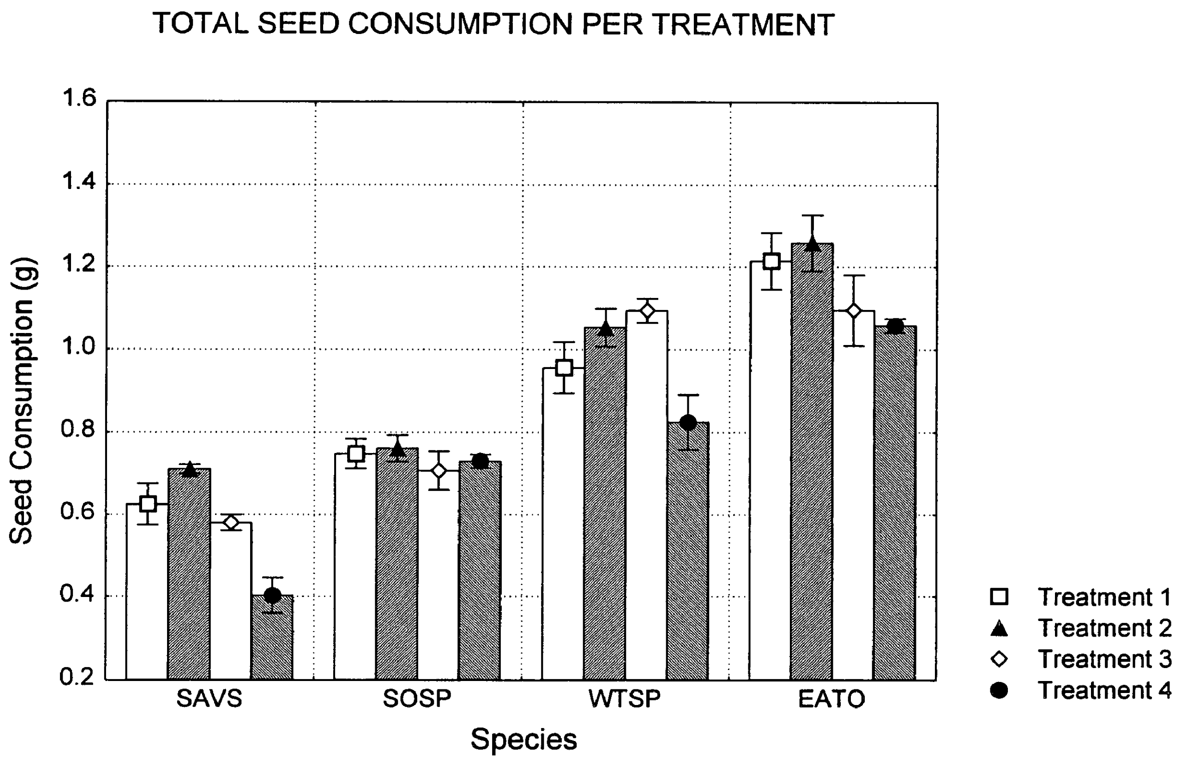
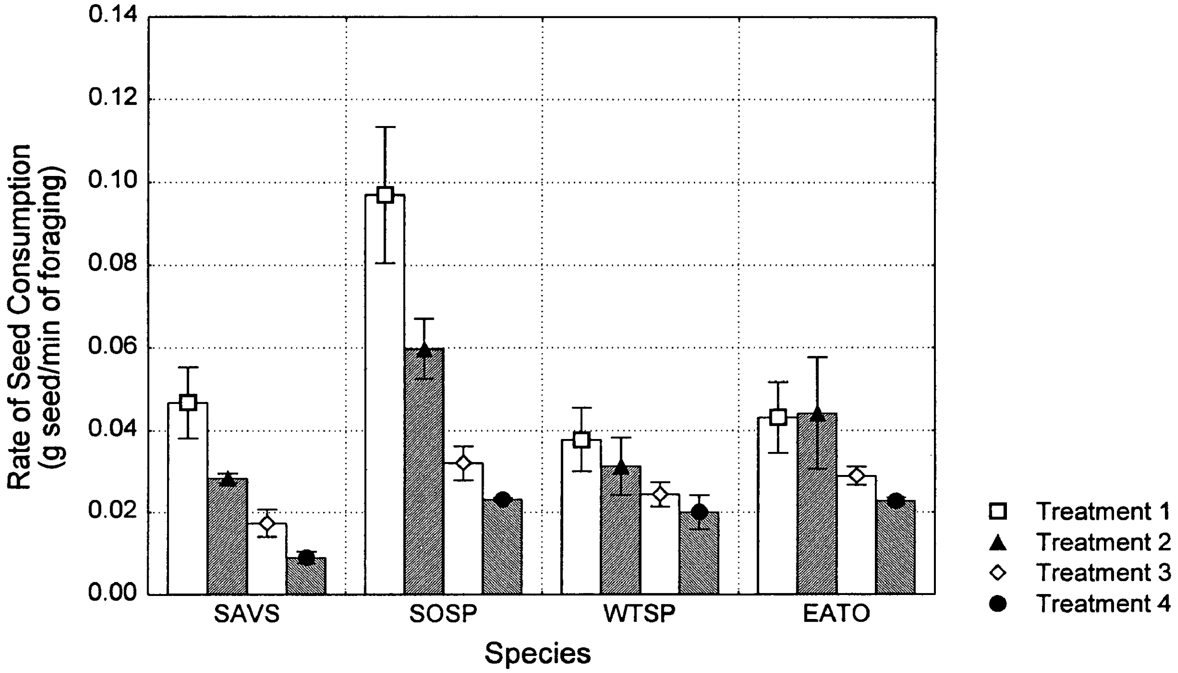

TOTAL SEED CONSUMPTION PER TREATMENT
Seed Consumption (g)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
SAVS
SOSP
WTSP
EATO
Species
□ Treatment 1
▲ Treatment 2
◇ Treatment 3
● Treatment 4

Figure 3. Mean rate of seed consumption (per minute of foraging time) by each species during each 90 min treatment. Whiskers indicate ± SE. SAVS=Savannah Sparrow; SOSP=Song Sparrow; WTSP=White-throated Sparrow; EATO=Eastern Towhee.



RATE OF SEED CONSUMPTION PER TREATMENT

Figure 4. Mean seed consumption (across all treatments) as a function of the log of body mass for each individual bird (four individuals per species). Regression line was fit with linear least squares. Dashed lines represent ± 95% confidence limits. SAVS=Savannah Sparrow; SOSP=Song Sparrow; WTSP=White-throated Sparrow; EATO=Eastern Towhee.

RELATIONSHIP BETWEEN SEED CONSUMPTION AND BODY MASS

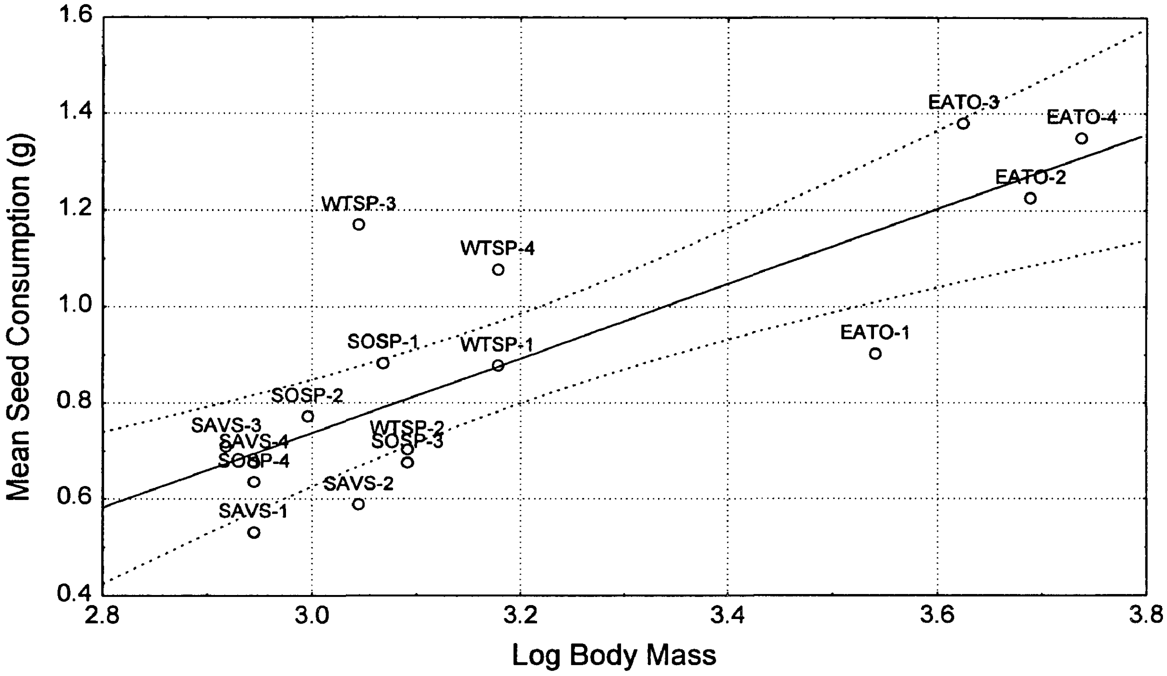
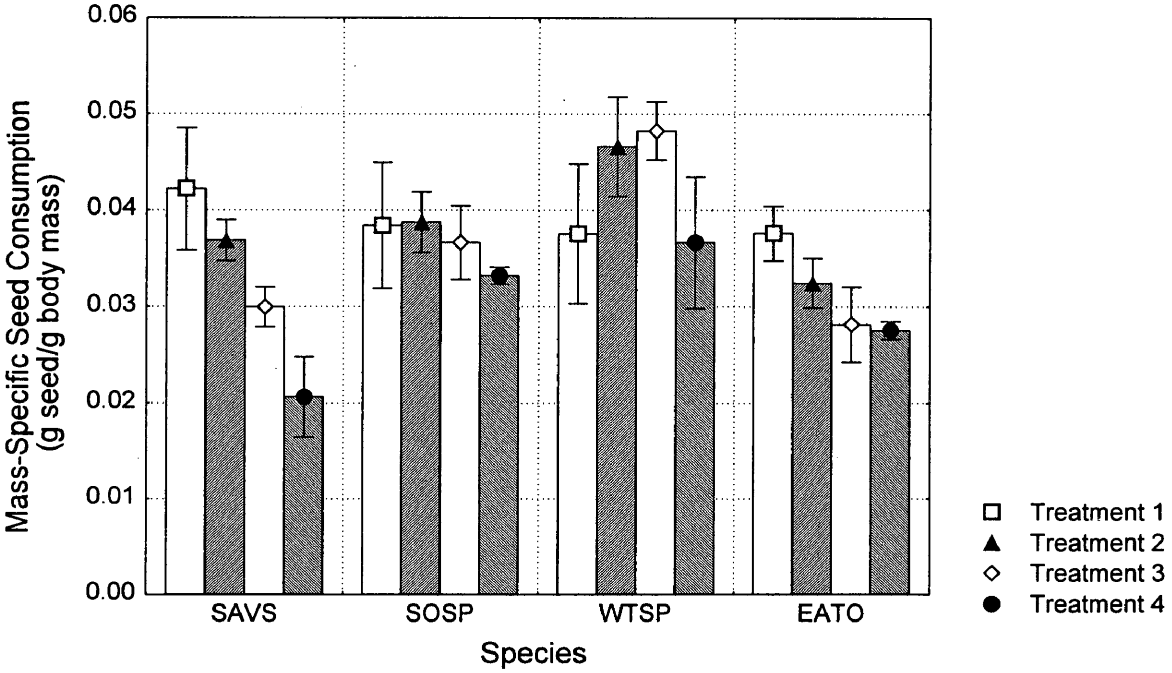


Figure 5. Mean body mass-specific seed consumption by each species during each 90 min treatment. Whiskers indicate ± SE. SAVS=Savannah Sparrow; SOSP=Song Sparrow; WTSP=White-throated Sparrow; EATO=Eastern Towhee.

BODY MASS-SPECIFIC SEED CONSUMPTION PER TREATMENT

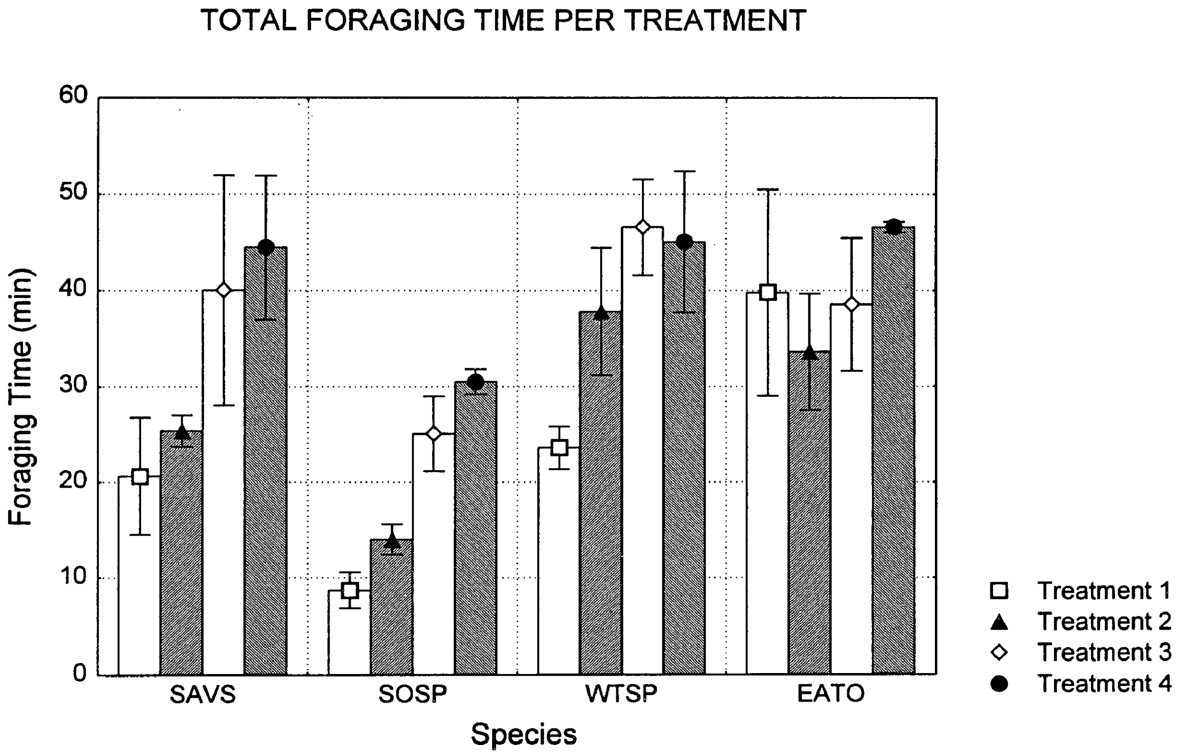


Foraging time (Figure 6) and the total number of scratches (Figure 7) did not differ among species. However, seed consumption per scratch did vary among species (Figure 8). Post-hoc comparisons (Tukey's tests) between species demonstrate that Eastern Towhees (the largest scratching species) consumed more seed per scratch than Savannah (P=0.003), Song (P=0.046), and White-throated (P=0.014) sparrows. Eastern Towhees uncovered more than 1.5 times as much seed per scratch than Song and White-throated sparrows and more than twice as much as Savannah Sparrows.

A summary of all repeated-measures ANOVA's of treatment effects is provided in Table 4. For all species combined, the following variables declined across treatments: total seed consumption (Figure 2), body mass-specific seed consumption (Figure 5), rate of seed consumption (Figure 3), and seed consumption per scratch (Figure 8). Increases across treatments occurred in foraging time (Figure 6) and the total number of scratches (Figure 7).

Interactions between species and treatment factors (see Table 4) were significant for the following variables: total seed consumption (Figure 2), body mass-specific seed consumption (Figure 5), and rate of seed consumption (Figure 3). All species responded in parallel across treatments to foraging time (Figure 6), total number of scratches (Figure 7), and seed consumption per scratch (Figure 8). Therefore interactions were not significant for these last three variables.

Figure 6. Mean time invested in foraging by each species during each 90 min treatment. Whiskers indicate ± SE. SAVS=Savannah Sparrow; SOSP=Song Sparrow; WTSP=White-throated Sparrow; EATO=Eastern Towhee.



TOTAL FORAGING TIME PER TREATMENT

Figure 7. Mean total number of scratches by each species during each 90 min treatment. Whiskers indicate ± SE. Results from all four treatments are presented here for graphical purposes. Treatments 1 and 2 were omitted from statistical analyses of scratching behavior in the text because birds could access seed without scratching during these treatments. SAVS=Savannah Sparrow; SOSP=Song Sparrow; WTSP=White-throated Sparrow; EATO=Eastern Towhee.

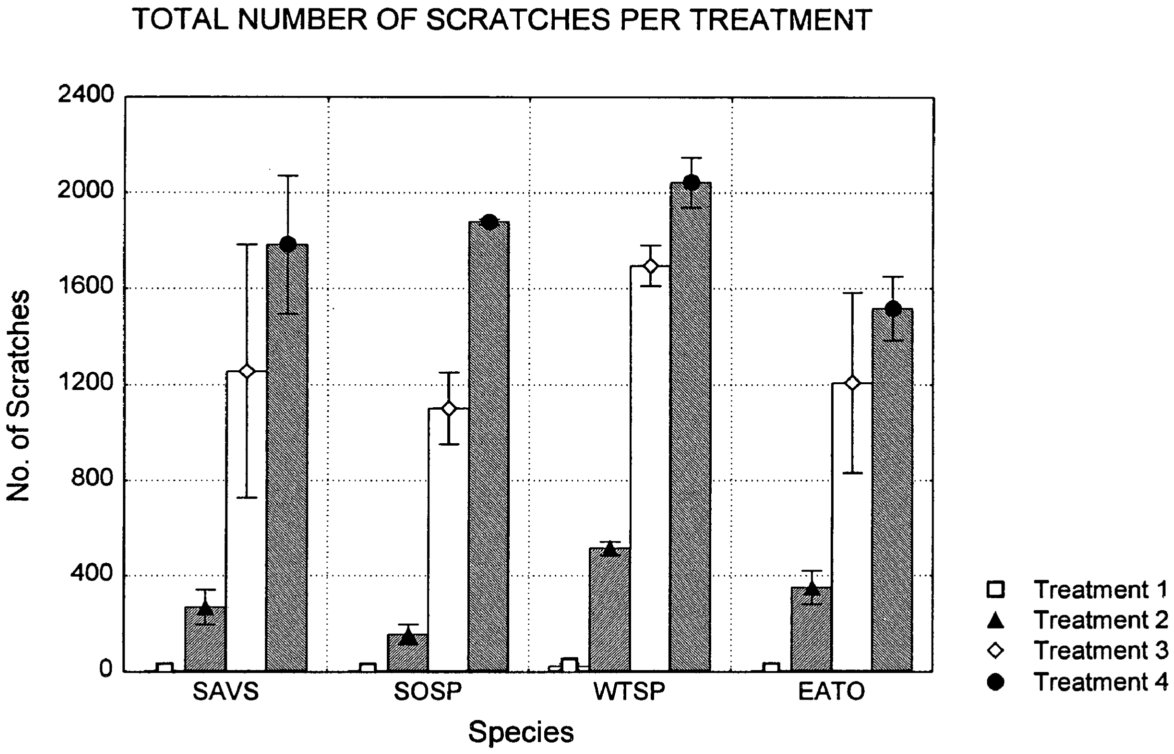
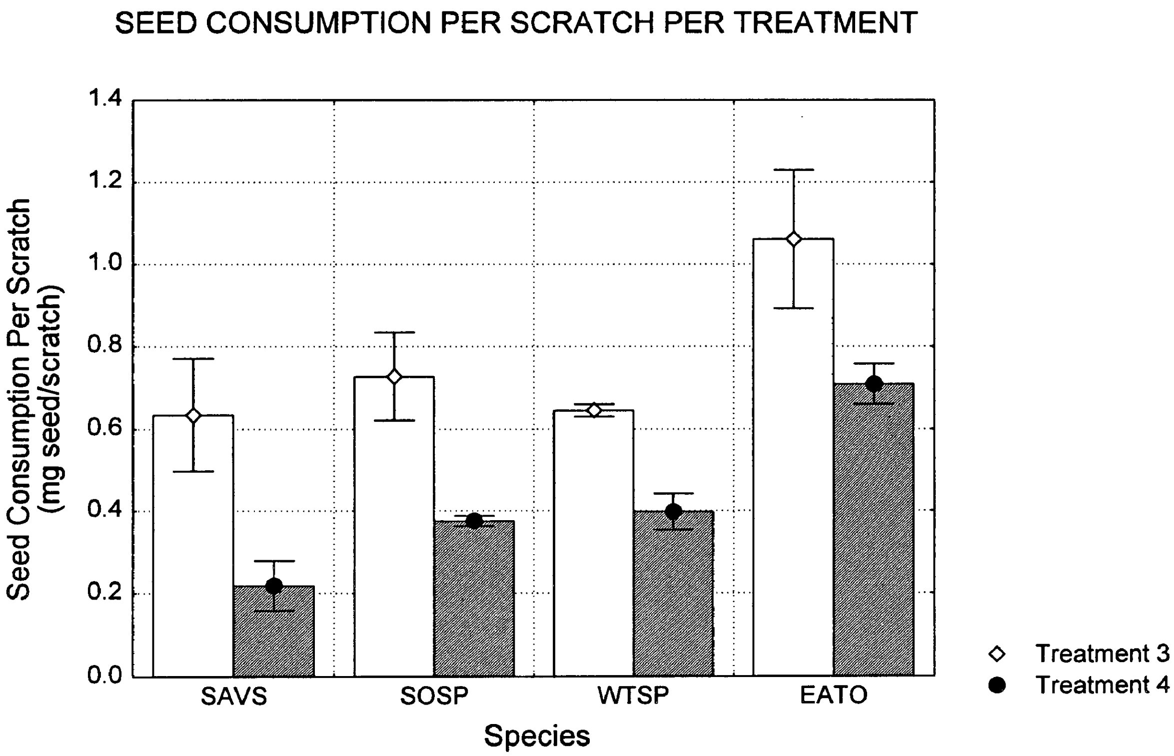

TOTAL NUMBER OF SCRATCHES PER TREATMENT
No. of Scratches
2400
2000
1600
1200
800
400
0
SAVS
SOSP
WTSP
EATO
Species
□ Treatment 1
▲ Treatment 2
◇ Treatment 3
● Treatment 4

Figure 8. Mean mass of seed consumed per scratch by each species during Treatments 3 and 4. Whiskers indicate ± SE. Treatments 1 and 2 are excluded because birds could access seed without scratching during these treatments. Note that a millet seed weighs approximately 6 mg. SAVS=Savannah Sparrow; SOSP=Song Sparrow; WTSP=White-throated Sparrow; EATO=Eastern Towhee.


SEED CONSUMPTION PER SCRATCH PER TREATMENT
Seed Consumption Per Scratch (mg seed/scratch)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
SAVS
SOSP
WTSP
EATO
Species
◇ Treatment 3
● Treatment 4

Savannah Sparrows Versus Song Sparrows

Results of pairwise comparisons between Savannah and Song sparrows within each treatment are presented in Table 5. These two species did not differ in the amount of seed consumed in each treatment except during Treatment 4 when Song Sparrows consumed nearly twice as much seed as Savannah Sparrows. In all treatments, Song Sparrows foraged at a faster rate than Savannah Sparrows, despite the fact that the amount of time spent foraging only differed between the two species during Treatment 2. Both species scratched at the same rate during Treatments 3 and 4, however, Song Sparrows managed to consume significantly more seed per scratch than Savannah Sparrows during Treatment 4.

Energetic Considerations

Based on energy budgets calculated from estimates of FMR required for maintenance, all species exceeded energetic requirements during Treatment 1 (Figure 9). Likewise, all species met energetic requirements during Treatment 2 except for Northern Cardinals which only achieved 67.9% (± 12.3%) of their required seed intake (Figure 10). Field Sparrows and Northern Cardinals failed to procure any seed during Treatments 3 and 4 because these species do not scratch. During Treatment 3, all scratching species exceeded 95% of their energetic requirements except for Savannah Sparrows (Figure 11). Mean energy intake for Savannah Sparrows was 85.3%

Table 5. Within-treatments pairwise comparisons of foraging performance between Savannah and Song sparrows.

	Variable	*t*-statistic	Significance level [a]	Direction of Difference [b]
Treatment 1				
	Seed consumption	-0.01	NS	none
	Rate of seed consumption	-2.92	*	SOSP > SAVS
	Foraging time	1.61	NS	none
Treatment 2				
	Seed consumption	-0.74	NS	none
	Rate of seed consumption	-2.93	*	SOSP > SAVS
	Foraging time	5.18	**	SAVS > SOSP
Treatment 3				
	Seed consumption	-1.23	NS	none
	Rate of seed consumption	-3.43	**	SOSP > SAVS
	Foraging time	1.42	NS	none
	No. of Scratches (Log transformed) [c]	0.54	NS	none
	Seed consumption per scratch	-0.90	NS	none

Table 5. continued.

	Variable	*t*-statistic	Significance level [a]	Direction of Difference [b]
Treatment 4				
	Seed consumption	-3.60	*	SOSP > SAVS
	Rate of seed consumption	-6.61	***	SOSP > SAVS
	Foraging time	1.96	NS	none
	No. of scratches	-0.28	NS	none
	Seed consumption per scratch	-2.93	*	SOSP > SAVS

[a] NS = non-significant, * $P < 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

[b] SAVS = Savannah Sparrow, SOSP = Song Sparrow.

[c] Log transformation was necessary to normalize the data

Figure 9. Mean energy budgets of six sparrow species during Treatment 1. Whiskers indicate ± SE. All seed was located on the soil surface during this treatment. Energy budgets were calculated as follows: energy budget = (seed consumed - seed required) / seed required. Seed requirements were based on a body mass-specific equation for field metabolic rates (FMR) in passerine birds (Nagy 1987). SAVS=Savannah Sparrow; SOSP=Song Sparrow; WTSP=White-throated Sparrow; EATO=Eastern Towhee; FISP=Field Sparrow; NOCA=Northern Cardinal.

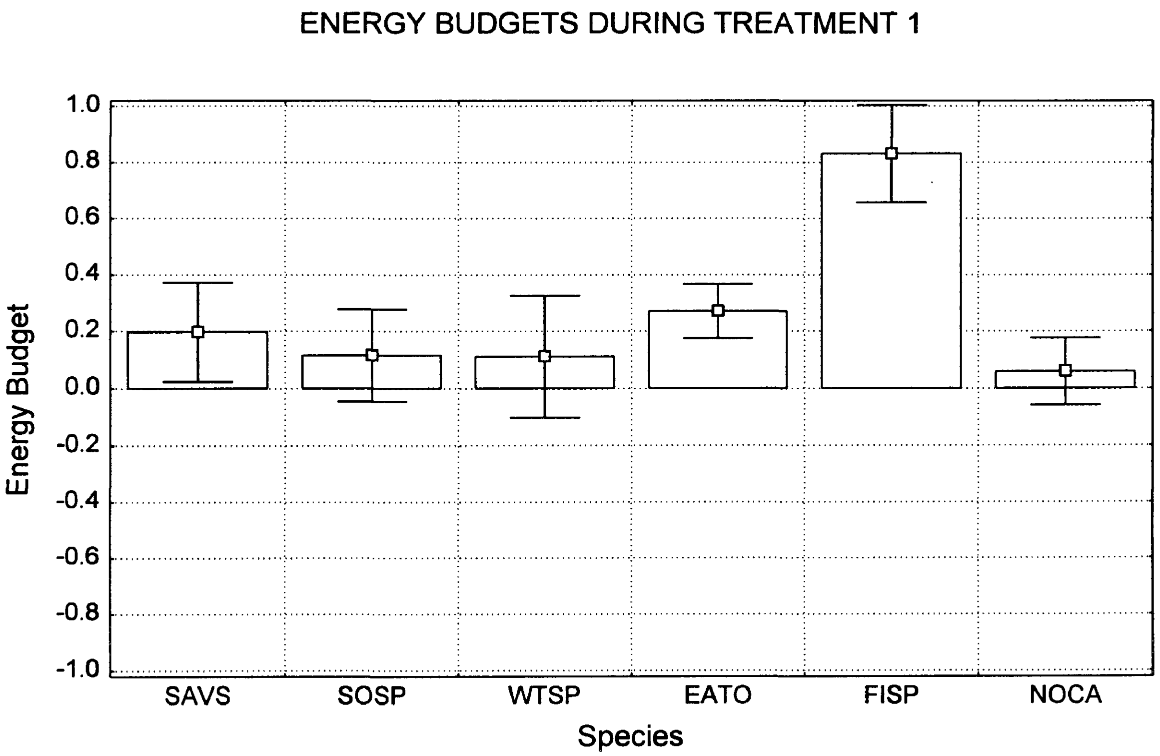

ENERGY BUDGETS DURING TREATMENT 1
Energy Budget
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
SAVS
SOSP
WTSP
EATO
FISP
NOCA
Species

Figure 10. Mean energy budgets of six sparrow species during Treatment 2. Whiskers indicate ± SE. All seed was located at a depth of 0.00-0.75 cm during this treatment. Energy budgets were calculated as follows: energy budget = (seed consumed - seed required) / seed required. Seed requirements were based on a body mass-specific equation for field metabolic rates (FMR) in passerine birds (Nagy 1987). SAVS=Savannah Sparrow; SOSP=Song Sparrow; WTSP=White-throated Sparrow; EATO=Eastern Towhee; FISP=Field Sparrow; NOCA=Northern Cardinal.

ENERGY BUDGETS DURING TREATMENT 2

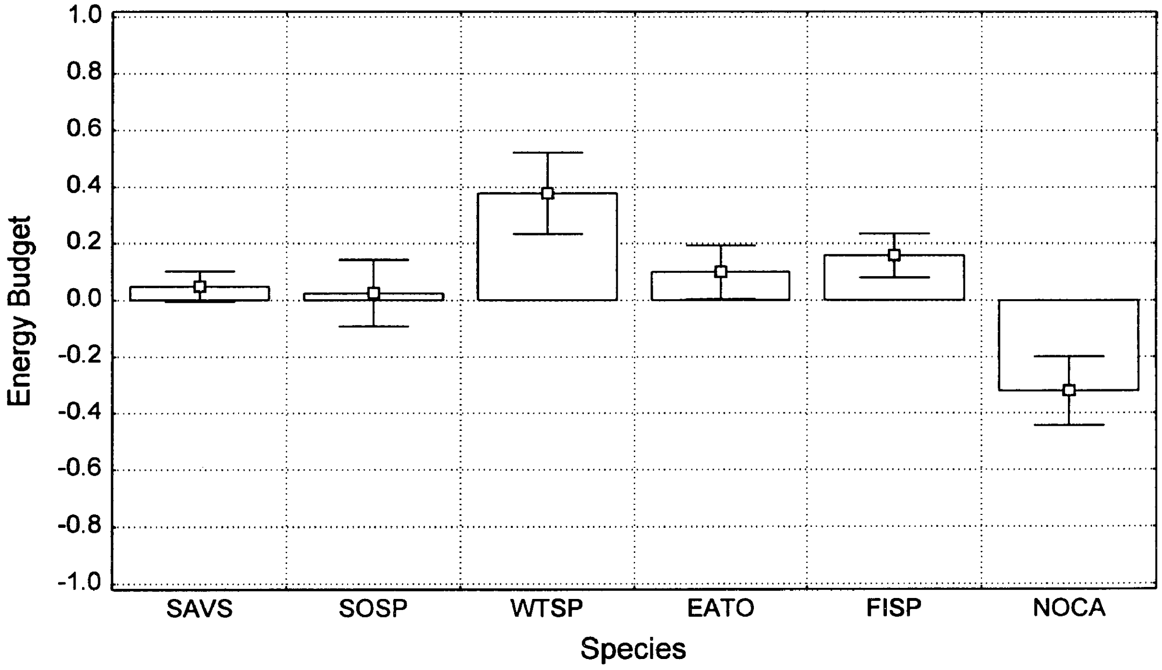
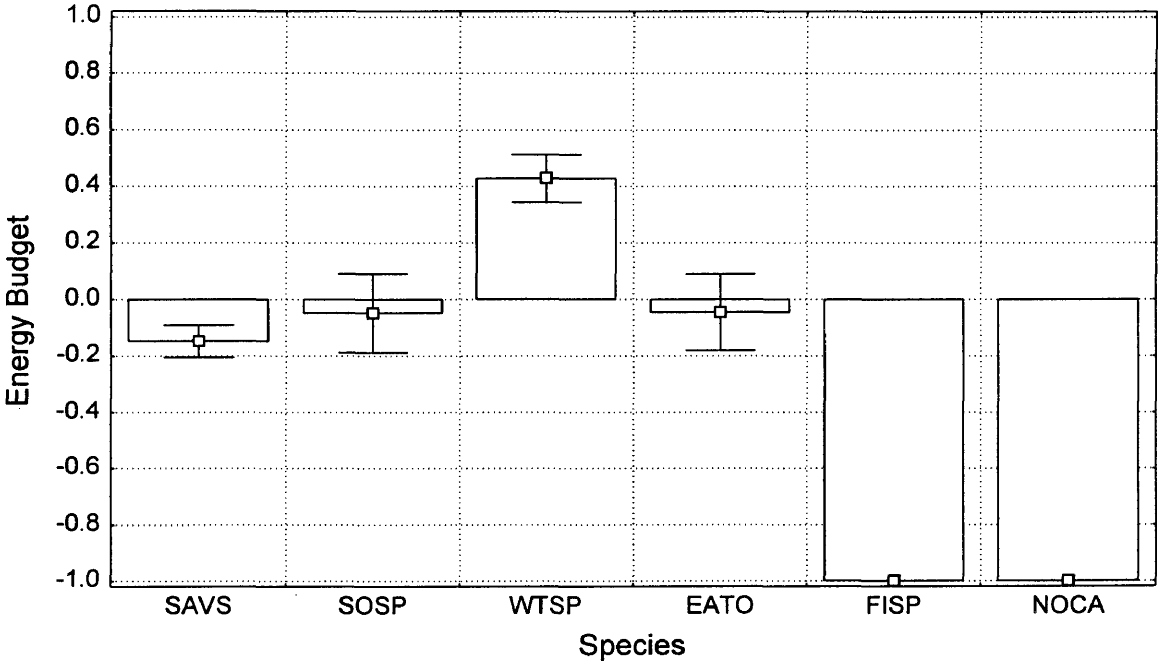


Figure 11. Mean energy budgets of six sparrow species during Treatment 3. Whiskers indicate ± SE. All seed was located at a depth of 0.75-1.50 cm during this treatment. Energy budgets were calculated as follows: energy budget = (seed consumed - seed required) / seed required. Seed requirements were based on a body mass-specific equation for field metabolic rates (FMR) in passerine birds (Nagy 1987). SAVS=Savannah Sparrow; SOSP=Song Sparrow; WTSP=White-throated Sparrow; EATO=Eastern Towhee; FISP=Field Sparrow; NOCA=Northern Cardinal.

ENERGY BUDGETS DURING TREATMENT 3



(± 5.76%) of their energetic requirement during Treatment 3. During Treatment 4, all scratching species exceeded 90% of their energetic requirements except for Savannah Sparrows which only met 60.4% (± 12.6%) of their required intake (Figure 12).

Figure 13 provides a comparison between Savannah and Song sparrows with energy budgets calculated from estimates of FMR required for maintenance and recalculated from theoretical estimates of maximum sustained FMR. Although both species would be more energetically stressed at maximum sustained rates, seed intake for Song Sparrows would still exceed 85% of their theoretical maximum requirements during all treatments. Seed intake for Savannah Sparrows, however, would fall to 74.9% (± 5.05) and 53.0% (± 11.1) of their maximum requirements during Treatments 3 and 4, respectively.

Figure 12. Mean energy budgets of six sparrow species during Treatment 4. Whiskers indicate ± SE. All seed was located at a depth of 1.50-2.25 cm during this treatment. Energy budgets were calculated as follows: energy budget = (seed consumed - seed required) / seed required. Seed requirements were based on a body mass-specific equation for field metabolic rates (FMR) in passerine birds (Nagy 1987). SAVS=Savannah Sparrow; SOSP=Song Sparrow; WTSP=White-throated Sparrow; EATO=Eastern Towhee; FISP=Field Sparrow; NOCA=Northern Cardinal.

ENERGY BUDGETS DURING TREATMENT 4

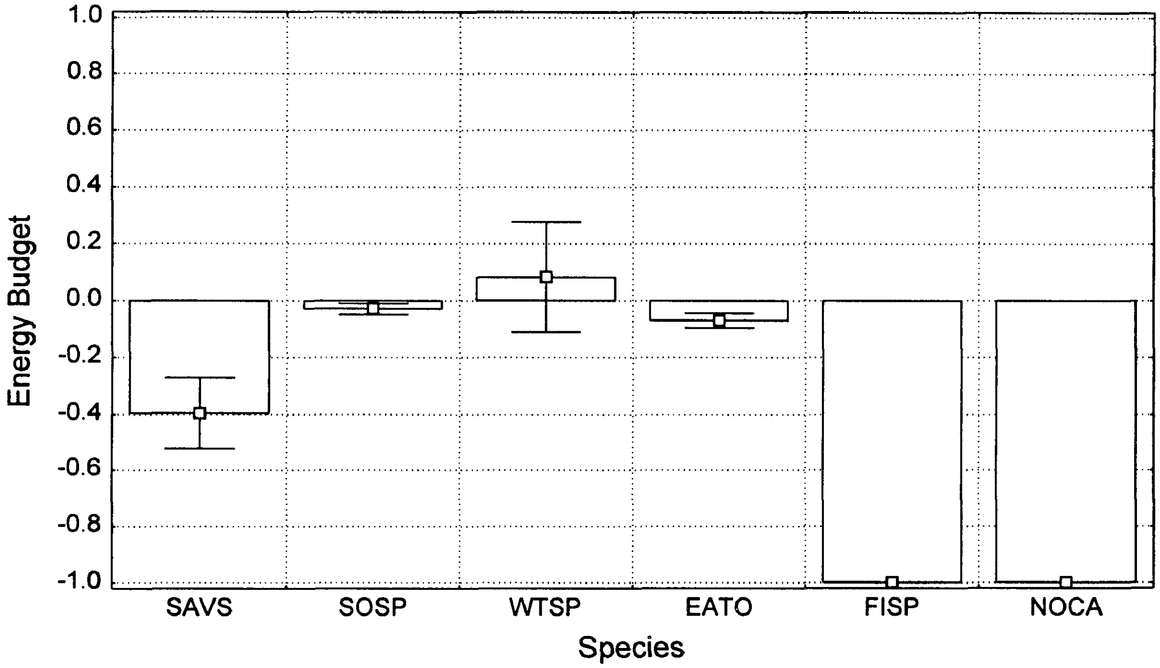
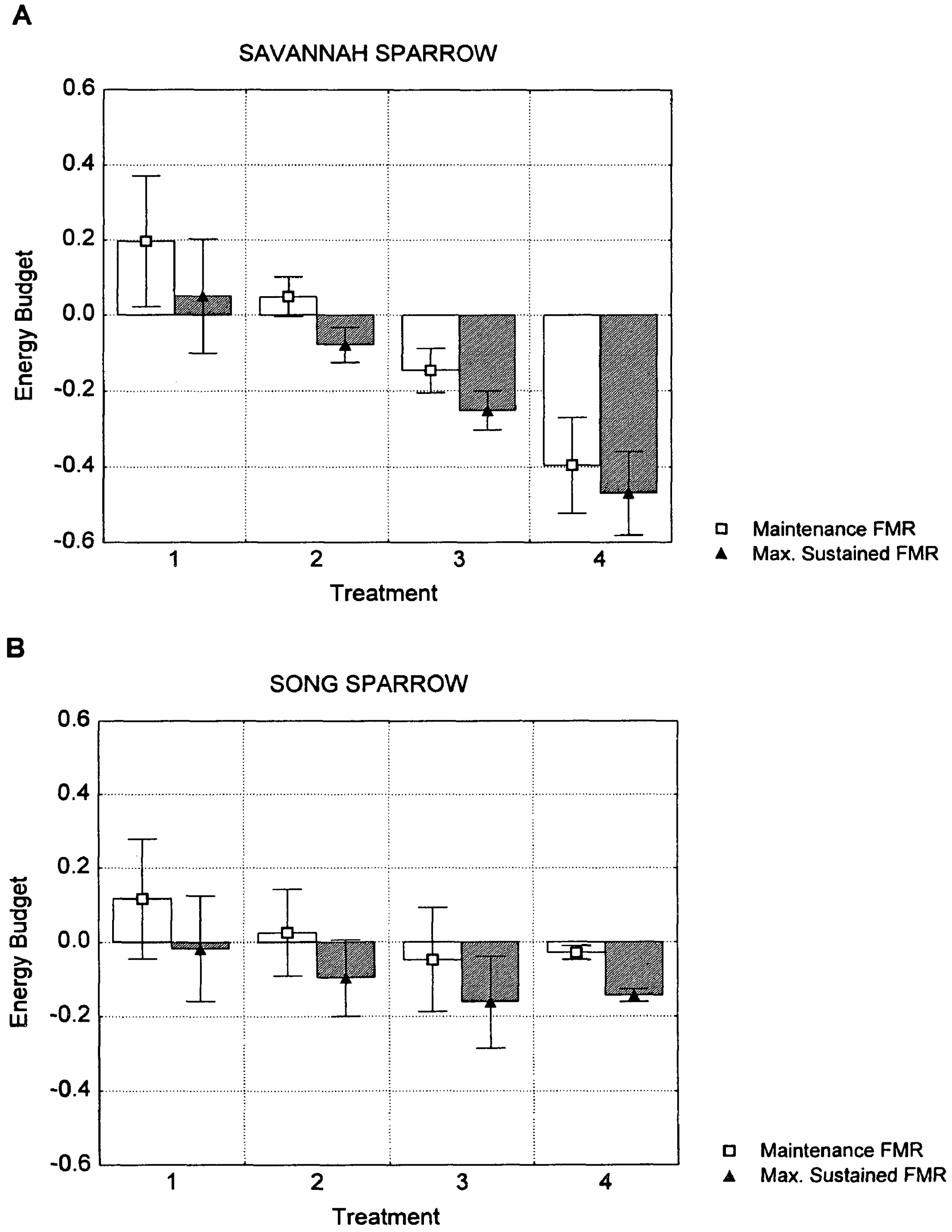


Figure 13. Mean energy budgets based on maintenance field metabolic rates (FMR) and maximum sustained FMR in (A) Savannah Sparrows and (B) Song Sparrows during all four treatments. Whiskers indicate ± SE. Energy budgets were calculated as follows: energy budget = (seed consumed - seed required) / seed required. Clear bars were based on seed requirements for field metabolic rates (FMR) calculated from Nagy (1987). Shaded bars were based on seed requirements for maximum sustained FMR which was assumed to be 3.0 x BMR. Values for BMR were calculated from Lasiewski and Dawson (1967).

ENERGY BUDGETS UNDER DIFFERENT LEVELS OF ENERGETIC DEMAND: SAVANNAH VERSUS SONG SPARROWS



DISCUSSION

This study provides quantitative data demonstrating interspecific variation in the bilateral scratching performance of sparrows. Differences were found in abilities to extract seed from soil and consequently in foraging efficiencies. Results suggest three functional groups based on relative scratching ability. Field Sparrows and Northern Cardinals were non-scratchers, Savannah Sparrows were weak scratchers, and Eastern Towhees, White-throated Sparrows, and Song Sparrows were strong scratchers.

Previous studies have suggested that scratching behavior is virtually absent in two species of the genus *Spizella*, Field Sparrow and Chipping Sparrow (*S. passerina*) (Clark 1970, Greenlaw 1977). In accordance with previous findings, Field Sparrows failed to scratch in the present study. Scratching behavior may not be required for these species because they both tend to forage on non-littered patches of ground or to glean seeds directly from the heads of standing grasses (Allaire and Fisher 1975). Interestingly, a third member of this genus, American Tree Sparrow (*S. arborea*) is known to scratch frequently (Greenlaw 1977). Unlike its congeneric relatives, however, American Tree Sparrows forage in microhabitats with abundant woody cover where litter typically occludes the soil surface (Naugler 1993).

Northern Cardinals also did not scratch in the present study and failed to meet their energetic requirements whenever seed was at least partially obstructed by soil. These results suggest that Northern Cardinals would be unable to persist through the winter by feeding exclusively on the seeds of grasses and forbs in habitats in which such seeds are buried by soil or litter. Unlike Field Sparrows, however, it is unlikely that large-bodied cardinals could meet their food requirements by gleaning small seeds from grass stems and the bare soil surface. Instead, wintering cardinals spend more than one-third of their foraging time in forested habitats where they consume relatively large food items such as fruits and non-grass seeds (Pulliam and Enders 1971). In dense woodland interiors, thick layers of broad-leaved litter are found and herbaceous seeds are scarce so scratching would be highly unproductive (Greenlaw 1977).

Although Savannah Sparrows scratched with the same frequency as the other scratching species, they accessed significantly less seed when foraging on seed buried below a depth of 1.5 cm in the soil. This suggests that scratches by Savannah Sparrows are less effective than the other species. This finding is not surprising in light of evidence that this species possesses proportionately less leg muscle mass than the other scratching species (B. D. Watts, personal communication). The consequence of weaker scratching ability was that Savannah Sparrows failed to meet their energetic requirements during treatments where seed was completely buried by soil. As a result, Savannah Sparrows probably cannot subsist by feeding exclusively in patches where seed is buried by soil or litter. Comparisons between energy budgets calculated from initial estimates of FMR and recalculated from estimates of maximum sustained FMR illustrate that, during periods of extreme low winter temperatures, Savannah Sparrows may be even more hard pressed to survive in habitats with little available surface seed.

Of all species tested, Eastern Towhees were clearly the most powerful scratchers. As relatively large-bodied sparrows that typically forage in microhabitats with abundant leaf litter, towhees are capable of moving substantial amounts of substrate with their feet. In fact, the foraging niche of large, ground-feeding, litter-scratching birds has been dubbed the "towhee niche" (Cody 1973). Despite their relatively high caloric requirements, towhees met or exceeded their energetic demands during all experimental treatments. Similarly, White-throated and Song sparrows experienced neutral or positive energy budgets in all treatments, suggesting that these species are also well adapted to foraging for buried seed.

The scratching ability of a given species may determine which foraging patches may be successfully exploited and how to cope with a declining seed supply. When all four treatments in the present study are considered in succession, the artificial food patches used are analogous to a single hypothetical food patch in which seed resources are initially distributed evenly across four layers in a vertical section of soil. As food resources are depleted in each layer, foragers must either scratch more deeply in the soil or search for a new patch. All non-scratching species must abandon any patch that no longer contains surface seed. Scratching species, on the other hand, can still access buried seed after surface seed has been depleted. The availability of buried seed resources, however, varies between species according to their relative scratching ability. As buried seed supplies are depleted by scratching species, weak scratchers will experience negative energy budgets sooner than strong scratchers.

The minimum resource density at which an individual should abandon a patch has been referred to as the giving-up density (GUD) (Brown 1988). In theory, GUD's are a reflection of the resource availability in a given patch. A relatively low GUD corresponds to relatively high resource availability. In a patch containing both superficial and buried seeds, it is expected that non-scratchers will have the highest GUD's, weak scratchers will have intermediate GUD's, and strong scratchers will have the lowest GUD's. Some empirical evidence supports this prediction. Marshall (1960) noted that Abert's Towhees (*Pipilo aberti*), which scratch frequently (Tweit and Finch 1994), spend more time foraging in a given spot than Canyon Towhees (*P. fuscus*), which are known as relatively weak scratchers (Davis 1957). Thus, Abert's Towhees apparently have lower GUD's and more potential resources available to them in a given patch than Canyon Towhees.

If strong scratchers can potentially forage more efficiently (i.e., to lower GUD's) than weak scratchers, how do these species coexist? Interspecific differences in foraging efficiencies at high and low resource densities may promote the coexistence of competing species within the same space (Abrams 1984). This mechanism of coexistence requires that each species possesses a unique resource density at which it is the most efficient forager. One competitor may be most efficient at foraging at high resource densities and thus abandon patches at high GUD's while another competitor may forage most efficiently on the remaining resources and abandon patches at low GUD's (Brown 1989). For example, Brown et al. (1997) suggested that Crested Larks (*Galerida cristata*) and gerbils (*Gerbillus allenbyi* and *G. pyramidum*) may coexist in the same habitats in the Negev Desert because larks function as the "cream skimmers" while gerbils function as the "crumb pickers". In the present study, strong scratchers had higher foraging efficiencies than the other species when seed was completely buried by soil. Thus these species may represent the "crumb pickers" when total resource densities are low. However, non-scratchers and weak scratchers did not forage at higher efficiencies than strong scratchers when surface seed was available. Since all species experienced high foraging rates on surface seed, competition for such resources should be intense. With all else being equal, strong scratchers would be expected to outcompete weak scratchers when resource densities fall below a certain level. Therefore, these results fail to support the coexistence of wintering sparrows based solely on differences in density-dependent resource consumption rates within the same microhabitats.

If the abundance of buried seeds varies between microhabitats, then species-specific differences in scratching ability may promote spatial partitioning of habitats. The prevalence of litter layers may produce such variation in the distribution of buried seed between habitats. Near woodland edges and deciduous shrubs, fresh litter accumulates concurrent with seed set from herbaceous plants each autumn. In open grassland habitats, on the other hand, litter is sparse and patches of bare soil are more abundant. The bulk of the emberizine species that are known bilateral scratchers use mixed grassland-shrub and/or woodland edge habitats rather than open grassland habitats (Greenlaw 1977). For example, Greenlaw (1977) stated that species that use shrub and woodland edges, such as Fox Sparrow (*Passerella iliaca*) and Rufous-sided Towhee (formerly *Pipilo erythrophthalmus*; this species was recently split into Eastern Towhee, *P. erythrophthalmus*, and Spotted Towhee, *P. maculatus*), were strong, effective scratchers while open grassland species such as Savannah Sparrow and Vesper Sparrow (*Pooecetes gramineus*) were weak scratchers. Thus, scratching ability does seem to vary with habitat preference.

Likewise, a comparison between White-throated Sparrows and Dark-eyed Juncos (*Junco hyemalis*) provides evidence for microhabitat selection between species that differ in scratching ability. Hailman (1974) found that

White-throated Sparrows generally scratch in longer bouts than Dark-eyed Juncos. However, when foraging in identical substrates, Dark-eyed Juncos were observed scratching in longer bouts than White-throated Sparrows. This apparent contradiction can be explained by differences in microhabitat preferences between these species. As stronger scratchers, White-throated Sparrows tend to forage in more heavily littered areas than Dark-eyed Juncos (Hailman 1984).

Varying scratching ability provides a simple mechanism to explain why weak scratchers should avoid habitats where most of the available seed is buried by soil or litter while strong scratchers may excel in such habitats. However, differences in scratching ability fail to explain why strong scratchers do not outcompete weak scratchers in all habitats where surface seed is limited. Theoretically, strong scratchers could forage more efficiently (i.e., to lower GUD's) than weak scratchers in any habitat where buried seed is available and surface seed is limited.

Numerous studies have documented the existence of habitat-specific tradeoffs between foraging efficiency and risk of predation (e.g., Grubb and Greenwald 1982, Kotler 1984, Lima 1985, Lima et al. 1985). These studies show that species may often forego food-rich patches if the risk of predation is high in these areas. Instead, species may select patches where the risk of predation is lower while suffering a cost of reduced resource availability. If a potential competitor species is better adapted to avoid predation, then this species may capitalize on the resources which are left unexploited in "high-risk" microhabitats. Hence, a tradeoff between foraging efficiency and risk of predation may promote the local coexistence of species.

Watts (1990) demonstrated that two of the species included in the present study, Song and Savannah sparrows, differ in relative risk of predation away from cover. In open habitats, Song Sparrows were more than 60 times more vulnerable to predators than were Savannah Sparrows. As a result, Song Sparrows show strong preferences to areas with abundant vegetative cover which provides a relative refuge from predation. Although many sparrow species use cover to minimize predation (see Lima 1993 for a review), some species may be better adapted than others at evading predators away from cover (Pulliam and Mills 1977, Lima and Valone 1991). For example, morphological evidence suggests that Savannah Sparrows are better adapted for aerial evasion of predators than Song Sparrows (B. D. Watts, personal communication). Savannah Sparrows have wings with a relatively high aspect ratio and are therefore well-suited to high-speed flight. In addition, this species possesses proportionately more flight muscle mass than Song Sparrows. As a result, Savannah Sparrows are less cover-dependent and can afford to forage away from cover in patches that Song Sparrows tend to avoid.

Strong scratching ability may be a necessary adaptation for species that are highly cover-dependent due to an inverse relationship between proximity to cover and the availability of surface seed. Since a large number of species use cover to minimize predation, resources in close proximity to cover are subject to intense demand. Watts (1996) found that both sparrow density and species richness are highest in plots adjacent to thick woody vegetation. As a result, surface seed may be most heavily exploited in areas that are close to cover. Woody vegetation serves not only as a source of cover but also as a source of litter. The thickest layers of litter accumulate near woodland edges and shrubs, both of which serve as the primary vegetative cover used by sparrows foraging in early successional habitats. Therefore, more seed resources may be buried by litter in areas near cover. The combination of intense resource competition and thick layers of leaf litter are likely to reduce the availability of surface seed near cover.

Each of the strong scratching species in the present study are highly cover-dependent. Both White-throated Sparrows and Eastern Towhees generally limit their foraging to areas in the immediate vicinity of woody vegetation (Schneider 1984, Greenlaw 1996). The vast majority of species listed by Lima (1993) as having predator escape tactics dependent on woody cover, are documented scratchers (Greenlaw 1977). Species that are described as independent of cover include the longspurs (*Calcarius* spp.), Lark Bunting (*Calamospiza melanocorys*), Snow Bunting (*Plectrophenax nivalis*), and McKay's Bunting (*P. hyperboreus*) (Lima 1993). Interestingly, scratching behavior is absent in each of these species (Greenlaw 1977). Between these extremes lie species that may use some combination of woody cover, herbaceous cover, and cover-independent tactics to evade predators. The present study demonstrates that one such species, Savannah Sparrows, can scratch, but that they do so less effectively than the cover-dependent species. Evidence suggests that Vesper Sparrows, another species known to use both herbaceous and woody vegetation (Lima 1993), also has intermediate scratching ability (Greenlaw 1977). Evidence of scratching behavior is generally lacking in sparrows of the genus *Ammodramus*. Members of this genus typically use open habitats with little or no woody vegetation (Grzybowski 1983, Dunning and Pulliam 1989, Rising 1996). Further investigations would be needed to confirm the existence of a general relationship between relative scratching ability and cover-dependency.

The potential relationship between scratching ability and patterns of habitat use is not restricted to birds. Small mammals also scratch or dig to access buried seed (Morgan and Price 1992). Cover-dependent quadrupedal rodents are more efficient at "scratch-digging" for buried seeds than are the less cover-dependent bipedal rodents (Morgan and Price 1992). However, bipeds can reach higher maximum speeds than quadrupeds (Djawdan and Garland 1988), and are thus better adapted to evading predators in open habitats. Brown (1989) suggested that a tradeoff between foraging efficiency and predation risk in bush versus open microhabitats could provide a mechanism of coexistence in desert rodent communities. The mechanism that

Brown proposed is analogous to the one outlined above for sparrow communities.

In conclusion, these results provide quantitative evidence of variation in the scratching ability of different sparrow species. Depending on the relative abundance of seed on the surface versus seed buried in soil, snow, or litter, scratching ability may determine which species can subsist in a given habitat. Strong scratching species may be at a competitive advantage to relatively weak scratchers in habitats with low surface seed densities. The availability of surface seed may be negatively correlated with proximity to cover due to resource competition and/or abundant litter. If so, a tradeoff between foraging efficiency and predation risk may permit the local coexistence of sparrows that vary in relative scratching ability and adaptations to evading predators.

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