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WINTER DIETS AND SEED SELECTION OF GRANIVOROUS BIRDS IN SOUTHWESTERN NEW MEXICO

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Abstract. We examined the diet of granivorous sparrows in winter through stomach and crop contents and compared seed consumption with availability, on grasslands of southwestern New Mexico during January–March 2003. We collected diet samples from 18 species of sparrows at five sites. Over 65 seed species were detected in diets. Despite high seed diversity in diets, five seed species accounted for 80% of seeds consumed. The most abundant seed species detected were perennial grasses sand and spike dropseed (*Sporobolus* spp.), annual grasses feather fingergrass (*Chloris virgata*), stinkgrass (*Eragrostis cilianensis*), and annual forbs amaranth (*Amaranthus* spp.), and carpetweed (*Mollugo verticillata*). The soil seed bank at these sites was also diverse with >90 species detected. The dominant seeds in the soil seedbank samples included feather fingergrass, stinkgrass, and carpetweed. Diets of coexisting species (Chipping Sparrow [*Spizella passerina*], Brewer's Sparrow [*Spizella breweri*], Vesper Sparrow [*Pooecetes gramineus*], Savannah Sparrow [*Passerculus sandwichensis*], and White-crowned [*Zonotrichia leucophrys*]) differed within the most diverse site and among sites. Dropseed seeds were the preferred seed type of the smaller-bodied *Spizella* sparrows and the larger-bodied Vesper Sparrow. Where present, dropseed was important in the diets of all sparrow species. Depending on location, cupgrass, amaranth, and dropseed were preferred by Savannah Sparrow while Vesper Sparrow preferred cupgrass, goosefoot (*Chenopodium* spp.), dropseed, and knotweed (*Polygonum* spp.). Small-bodied sparrows specialized on small-sized seeds whereas larger-bodied sparrows exhibited preferences for seeds representing a diversity of sizes. The importance of the perennial dropseed grasses in sparrow diets emphasizes the need to examine the influence of management practices on seed production for this grassland type.

Key words: arid environments, diet, dropseed, emberizid sparrows, granivore, seed bank, seed selection, *Sporobolus*, southwestern grasslands, winter avifauna.

DIETA INVERNAL Y SELECCION DE SEMILLAS POR AVES GRANIVORAS EN EL SUROESTE DE NUEVO MEXICO

Resumen. Analizamos la dieta invernal de gorriones granivoros a traves de contenidos estomacales y de mollejas, y comparamos el consumo de semillas con su disponibilidad en pastizales del Suroeste de Nuevo Mexico durante Enero a Marzo de 2003. Colectamos muestras de la dieta de 18 especies de gorriones en cinco areas. Mas de 65 tipos de semillas fueron detectados en las dietas. A pesar de la alta diversidad de semillas encontradas, solo cinco tipos representaron el 80% de las semillas totales consumidas por las aves. Las semillas mas abundantes fueron las de pastos perenes arenosos y zacaton (*Sporobolus* spp.), pastos anuales pata de gallo (*Chloris virgata*), pasto hediondo (*Eragrostis cilianensis*), ataco anual (*Amaranthus* spp.) y alfombrilla (*Mollugo verticillata*). El banco de semillas en el suelo de los sitios tambien fue diverso, encontrando mas de 90 especies. Los tipos dominantes en las muestras de los bancos de semillas incluyeron pata de gallo, pasto hediondo y alfombrilla. Las dietas de especies simpatricas (gorrion ceja blanca [*Spizella passerina*], gorrion de Brewer [*Spizella breweri*], gorrion cola blanca [*Pooecetes gramineus*], gorrion savanero [*Passerculus sandwichensis*] y el gorrion corona blanca [*Zonotrichia leucophrys*]) difirieron dentro de los sitios mas diversos y entre las diferentes areas. Las semillas de zacaton fueron las preferidas por los gorriones de cuerpo mas pequeño del genero *Spizella* y por los gorriones de cola blanca, de cuerpo mas grande. Cuando estuvo presente, el zacaton fue importante en la dieta de todas las especies de gorriones. Dependiendo del sitio, el zacate fortuna (*Eriochloa* spp.), ataco y zacaton fueron preferidos por gorriones savaneros, mientras que el gorrion de cola blanca prefirio zacate fortuna, quinoa (*Chenopodium spp*.), zacaton y sanguinaria (*Polygonum* spp.). Los gorriones de cuerpo pequeño se especializaron en semillas de tamaño pequeño, mientras que los gorriones de cuerpo grande exhibieron preferencias por semillas de diversos tamaños. La importancia de los pastizales de zacaton perene en la dieta de los gorriones enfatiza la necesidad de examinar la influencia de las practicas de manejo sobre la produccion de semillas para este tipo de pastizales.

The production and distribution of seed resources are among the most important factors influencing the winter abundance and diversity of granivorous birds in arid and semi-arid environments (Grant 1966, Schluter and Repasky 1991, Blendinger and Ojeda 2001, Moorcroft et al. 2002). Unpredictable rainfall events result in a patchy distribution of seeds that varies substantially across years. Tracking resources at a landscape scale allows granivorous birds to select winter locations that will best meet their energy demands. Once established at a winter location, some species have been found to be mainly sedentary in nature, maintaining small home ranges (Gordon 2000, Ginter and Desmond 2005) while other species are thought to be highly mobile, tracking resources across a larger scale (Gordon 2000, Blendinger and Ojeda 2001). However, because little information is available on the diets of these birds and seed availability at foraging sites, the attributes of the seed supply that actually drive avian distribution and abundance are not well understood. This lack of information is due, in part, to difficulties in determining diet (Rosenberg and Cooper 1988).

Several studies have reported positive relationships between winter sparrow abundance and seed abundance, suggesting sparrows cue in on overall seed production (Pulliam and Parker 1979, Dunning and Brown 1982, Grzybowski 1983, Ginter and Desmond 2005). For example, Grzybowski (1983) found a positive correlation between seed production and avian abundance in winter in southwest Texas, and Ginter and Desmond (2005) found higher seed biomass during the winter on plots in south Texas where Savannah Sparrows (*Passerculus sandwichensis*) foraged (based on radio-telemetry data) compared to randomly selected plots. Dunning and Brown (1982) found winter sparrow abundance from 21 yr of Christmas bird count data to be positively correlated with monsoonal rainfall from the preceding summer, a predictor of seed production. However, Pulliam and Dunning (1987) found no relationship between sparrow abundance and seed production during 2 yr of moderate seed production and suggested the density of winter sparrows is independent of seed abundance in years where production is moderate to high.

Other studies suggest birds cue in on specific seed species (Pulliam 1986, Niemela 2002, Cueto et al. 2006), sometimes showing a preference for forb or grass seeds. Seed size, morphology, nutrient content, coat thickness, visibility, and secondary chemical compounds may all influence seed selection (Pulliam and Brand 1975, Greig-Smith and Wilson 1985, Diaz 1990, van der Meij and Bout 2000). Pulliam (1985) reports that small-bodied sparrows are more efficient at handling small seeds whereas large-bodied sparrows are equally efficient at handling large and small seeds. Niemela (2002) found a positive correlation between winter Horned Lark (*Eremophila alpestris*) abundance and the abundance of *Sporobolus* spp. seeds, and between Brewer's Sparrow (*Spizella breweri*) abundance and the abundance of buckwheat (*Eriogonum* spp.) seeds on study sites in southern New Mexico, possibly indicating these birds were responding to the abundance of these specific seed species. Pulliam (1980) found the majority of seeds in Chipping Sparrow (*Spizella passerina*) diets to be from forbs, with the three most common seeds comprising of one grass species, Lehmann lovegrass (*Eragrostis lehmanniana*), and the forbs amaranth (*Amaranthus retroflexus*), and buckwheat (*Portulaca* spp.). Interestingly, Pulliam (1985) found that Lehmann lovegrass and buckwheat seeds were abundant in the seed bank, whereas amaranth seed was substantially less abundant. In arid parts of Argentina, granivorous birds were found to select grass over forb seeds (Marone et al. 1998, Cueto et al. 2006), and seed biomass was important, with sparrows exhibiting a preference for larger-sized grass seeds (Cueto et al. 2006). Cueto et al. (2006), however, observed that granivorous sparrows exhibited variation in seed preference, or avoidance of certain seed types, despite similarity in seed dimensions, suggesting that factors other than size alone, such as energy content (Gluck 1985), may influence seed choice.

Availability of specific seed species is influenced by rainfall pattern and season. In the arid Southwest, winter and spring rains are likely to trigger the production of forbs, whereas grass seed is produced in response to late summer monsoonal rains (Pulliam and Brand 1975). The resulting differences in seed production among years and across sites will likely result in substantial differences in sparrow diets. Pulliam (1980) found that Chipping Sparrows did not consume seeds in relation to availability following a year of high monsoonal summer rainfall and suggested sparrows maximize their rate of energy intake by selecting seeds of higher value. Pulliam (1985, 1986) hypothesized that a broad overlap in sparrow diets would exist when seeds were scarce and they would specialize or be more selective in years of moderate to high seed production. Differences in seed consumption in relation to availability for Chipping Sparrows was attributed to the toxic nature of some seed species and the high nutrient value of others (Pulliam 1980).

Few studies have examined winter emberizid sparrow diets in detail, especially comparisons of avian diet to seed availability within and among sites. We studied the diets of winter sparrows under natural conditions at five grassland sites in southern New Mexico. We examined the relative importance of different seed types including forb, annual grass, and perennial grass seeds, and we examined the influence of seed abundance and diversity on community dynamics of winter emberizid sparrows. We tested two related hypotheses: (1) coexisting sparrow species consume seed resources differently within sites and, (2) individual species consume seed resources differently among sites. To test these hypotheses we compared diets of sparrows within and among sites and examined seed selection in relation to winter avian community composition and the composition of the seed bank. Understanding seed preference and the influence of seed abundance and distribution on avian abundance and community composition is important to the conservation and management of desert grasslands and their associated avifauna.

METHODS

Study Area

Study sites were located in Hidalgo County, southwestern New Mexico, within the 130,000 ha Diamond A Ranch operated by the Animas Foundation. Wintering birds tend to congregate in the vicinity of cattle watering sites (shallow ponds filled with rain water, troughs, and/or above ground tanks), therefore we chose five study sites near water sources to maximize sampling effort. We have observed that a wide variety of sparrows (Chipping, Brewer's, Vesper [*Pooeceets gramineus*], Savannah, Grasshopper [*Ammodramus savannarum*], and Baird's [*Ammodramus bairdii*]) readily use these types of sites. Field observations at our study sites confirmed that sparrows congregating in the vicinity of these sites were also foraging in the vicinity of these sites. Site locations included a variety of habitats, primarily open grassland, shrub-dominated, and disturbed habitats (Table 1).

DATA COLLECTION

Birds were captured using mist-nets during January–March 2003, from 0730 through 1700 H depending on the weather conditions. All five sites were sampled in mid-winter (January to mid-February); three sites (3–5) were

TABLE 1. Study site descriptions and species present on the respective sites.

Site	Description	Species present [a]
Site 1	Open grassland dominated by annual grasses and forbs. Water source was a depression in the ground approximately 0.25 ha and 50 m from nets.	Horned Lark (*Eremophila alpestris*) Vesper Sparrow (*Pooecetes gramineus*) Savannah Sparrow (*Passerculus sandwichensis*)
Site 2	Mixed grassland with dense cholla (*Opuntia imbricata*) patches, surrounded by oak (*Quercus* spp.) woodland. Water sources were a depression in the ground and an above ground steel tank separated by 10 m. Nets were 30 m from water sources.	Botteri's Sparrow (*Aimophila botterii*) Vesper Sparrow Black-throated Sparrow (*Amphispiza bilineata*) Grasshopper Sparrow (*Ammodramus savannarum*)
Site 3	Open mixed grassland with both perennial and annual grasses at the transition zone with a juniper-oak (*Juniperus* spp.-*Quercus* spp.) woodland. Water site was an above ground steel tank, 300 m from nets.	Mourning Dove (*Zenaida macroura*) Chipping Sparrow (*Spizella passerina*) Brewer's Sparrow (*Spizella breweri*) Vesper Sparrow Lark Bunting (*Calamospiza melanocorys*) Savannah Sparrow White-crowned Sparrow (*Zonotrichia leucophrys*) Dark-eyed Junco (*Junco hyemalis*) Chestnut-collared Longspur (*Calcarius ornatus*) House Finch (*Carpodacus mexicanus*) House Sparrow (*Passer domesticus*)
Site 4	Disturbed weedy patch surrounded by open grassland dominated by blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactiloydes*), and dropseed (*Sporobolus* sp.). Water source was an above ground steel tank, 50 m from nets.	Vesper Sparrow Savannah Sparrow Grasshopper Sparrow
Site 5	Disturbed weedy patch surrounded by riparian vegetation and scattered bottom land grassland patches. Water sources were a concrete tank and adjacent ground level water troughs, 10 m from nets.	Vesper Sparrow Savannah Sparrow Chipping Sparrow Dark-eyed Junco Lincoln Sparrow (*Melospiza lincolnii*) Western Meadowlark (*Sturnella neglecta*)

[a] Diet analysis was only conducted on the five most common species (Brewer's, Chipping, Savannah, Vepser, and White-crowned Sparrows).

re-sampled in late-winter (late-February to mid-March). However, additional birds were captured only at site 3. Each bird was induced to regurgitate stomach and crop contents by flushing the stomach with warm water (Ford et al. 1982). Seeds from avian stomachs and crops were regurgitated onto a coffee filter which was folded and stored in a manila envelope until the seeds were counted and identified. All birds were banded with USGS bands to avoid re-sampling on the same day.

To estimate seed availability, we collected 20 random soil seed bank samples within each site during mist netting events in mid-winter. A second set of seed bank samples was collected in late-winter at the three sites that were re-sampled for birds during late-winter. Soil seed samples were taken using an aluminum can of 8.8 cm in diameter inserted to a depth of 0.5 cm, collecting a total volume of 30 cc (Pulliam 1980, 1986; Ginter and Desmond 2005). Seeds were separated from soil using a hydropneumatic root elutriator, a machine that has been specifically adapted and used to separate seeds from soil samples by using air and water pressure to separate organic and inorganic materials (Gross and Renner 1989). A thin layer of soil remains following the separation process, so samples were sieved onto a grid-pattern Petri-dish in order to conduct the final seed separation and to count all seeds. This process was repeated as many times as needed for each sample. Seeds in soil and avian diet samples were counted using a 10 x 40 power stereoscope.

To determine the weight of seed species, we consulted the values of seed mass in the literature (Pulliam and Brand 1975; Pulliam 1985, 1986; Pulliam and Dunning 1987) and also weighed seeds in the laboratory using a Mettler AE160 balance. Harper et al. (1970) reported a high degree of constancy in the mean weight of seed grains within species in a wide range of plants. We also observed this and assumed a uniform weight for all seeds of a given species. We used the weight (mg) of each seed species to estimate the seed biomass by unit area (kg/ha) for each of the five sites and to estimate the relative importance of all seed species in the avian diets at each site. We estimated the proportional abundance (% biomass) of seed species at each site and the proportion of seed consumed (% biomass) by the different bird species at each site. We also estimated the total biomass (kg/ha) of all seeds in the seed bank.

Statistical Analysis

To examine if soil seed bank biomass differed among sites within mid- and late-winter periods, we used analysis of variance (ANOVA) and post hoc least significant difference (LSD) tests. To determine if winter sparrows were feeding on seeds relative to availability or were being selective (showing a preference) at individual sites, we compared seed consumption (biomass) from stomach and crop regurgitation to seed availability from the soil seed bank samples (biomass) using Johnson's rank preference (Johnson 1980). Johnson's rank preference method orders food items (seed species) in a ranking system from most preferred to least preferred (or most avoided). This method also determines if significant differences exist in the preference of specific seed species consumed by individual avian species at a site. The statistical software PREFER v5.1 (Pankratz 1994) was used to perform all calculations. Two analyses were conducted for the five most common bird species in mid-winter (Chipping, Brewer's, Vesper, Savannah, and White-crowned [*Zonotrichia leucophrys*] Sparrows): first for all five species at the single site where all of them were found; then for the two most broadly distributed species across sites. In addition, this analysis was conducted on four species—Chipping, Brewer's, Vesper, and Savannah Sparrows—at a single site, comparing mid-winter with late-winter diets. We used a minimum of six diet samples for each species to conduct diet analysis. All seeds with percentages less than 5% in both the soil and avian diets were excluded from the analysis at each site.

To test the hypothesis that coexisting sparrow species consume seeds differently, we performed multivariate analyses of variance (MANOVA) to assess the differences in seed species selection, based on biomass, (SAS Institute 1990) among the same five most common sparrows within site 3. We performed individual ANOVA and post hoc LSD tests to determine where significant differences were located.

RESULTS

Precipitation was 9.78 cm below normal for 2002 and 0.13 cm above normal for early 2003. Monthly precipitation totals in late 2002 (particularly October) were above normal and may have contributed to the observed intermediate and high seed production (NOAA 2002, 2003).

The soil seed bank at the five sites was diverse, with over 90 seed species detected. Overall, dominant seeds (by biomass) included feather fingergrass (*Chloris virgata*), stinkgrass (*Eragrostis cilianensis*), and carpetweed (*Mollugo verticillata*). We collected 609 diet samples from

573 individual birds of 18 species between January and March 2003 across the five sites (Table 1). Several individuals were recaptured and resampled during the winter. We detected over 65 seed species in diets and a small number of seedlings and invertebrates. Overall, the most abundant seed species (as determined by biomass) detected in avian diets were perennial grasses including sand and spike dropseed (23% biomass), annual grasses including feather fingergrass (24%) and stinkgrass (8%), and annual forbs including amaranth (18%) and carpetweed (6%).

We examined the diets (based on biomass) of the five most common avian species within and among study sites. Chipping Sparrow (N = 60) was present at only two sites. We found 23 seed species in their stomach and crop contents, with five species (dropseed, feather fingergrass, carpetweed, threeawn [*Aristida* spp.], and amaranth) comprising 73% of their diet. Brewer's Sparrow (N = 37) was present at just one site, with 15 seed species in their stomach/crop contents, of which four seed species (dropseed, amaranth, feather fingergrass, and threeawn) comprised over 72% of their diet. Vesper Sparrow (N = 148) was present at all five sites, but only in sufficient numbers for sampling at four of the sites. Fifty-six seed species were detected in their stomach and crop contents, with five species (amaranth, cupgrass, dropseed, feather fingergrass, and panicum [*Panicum* spp.]) accounting for 59% of their diet. Savannah Sparrow was the most abundant species sampled (N = 270) and was present at four of the five sites. We detected 47 seed species in Savannah Sparrow stomach/crop contents, with five seed species (amaranth, feather fingergrass, cupgrass, stinkgrass, and dropseed) comprising over 78% of their diet. White-crowned Sparrow (N = 44) was present at only one site, with 15 seed species in their stomach/crop contents, of which two seed species (amaranth and dropseed) comprised 79% of their diet.

Soil Seed Bank

Seed biomass from soil seed bank samples taken in mid-winter differed significantly among sites, as did seed biomass in late-winter (Table 2). Seed resources (biomass) were significantly greater at sites 1 and 3 with respect to the other sites ($P < 0.05$, Table 2) in mid-winter; resources were significantly greater at site 3 with respect to the other two sites ($P < 0.05$; Table 2) in late-winter. Site 3 had high biomass and intermediate diversity of seed resources and, based on mist netting efforts, appeared to support the highest abundance and diversity of birds. Site 1, in comparison, had a high biomass but low diversity of seeds; this site did not appear to support a large diversity or abundance of birds and did not have perennial grass seed production. We observed a decrease in seed biomass over time at the three sites where the soil seed bank was sampled again in late winter. Mean seed biomass decreased by 50% at site 3, 53% in site 4 and 44% at site 5 (Table 2).

Diets of Coexisting Sparrows

The diets of different bird species pooled across mid- and late-winter, based on percent biomass, differed significantly at site 3 (MANOVA: $F = 4.62$, df = 40, $P < 0.01$), the site with the highest diversity and abundance of birds and a high biomass and intermediate diversity of seeds. Individual ANOVAs were performed to identify the specifics of those differences in seed consumption among bird species (Table 3). We found significant differences in consumption of dropseed grass seeds among sparrows, with Brewer's Sparrows consuming significantly higher proportions than Savannah and White-crowned Sparrows. Chipping Sparrows consumed more threeawn seeds than Savannah, Vesper, and White-crowned Sparrows. Savannah Sparrows consumed significantly higher proportions of cupgrass than all

TABLE 2. Comparisons of soil seed bank—mean (sd) biomass (kg/ha), species richness, and Shannon-Weiner diversity index (H'; Zar 1999)—at five sites during mid-winter (January–mid-February 2003) and at three sites during late-winter (late February–mid–March 2003). Species richness and diversity were calculated with data pooled across mid- and late-winter periods.

Site	Mid-winter [a]	Late-winter [b]	Richness	H′
Site 1	141.5 (104.2)[c]		24	1.4
Site 2	60.2 (40.7)[d]		33	2.5
Site 3	114.5 (82.4)[c]	56.8 (50.2)[c]	39	2.1
Site 4	67.9 (48.2)[d]	32.2 (20.7)[d]	40	1.9
Site 5	41.2 (27.5)[d]	23.1 (23.2)[d]	44	2.4

[a] $F = 7.68_{4,95}$, $P < 0.01$.
[b] $F = 5.25_{2,57}$, $P < 0.01$.
Note: Means with the same superscript within a column did not differ significantly ($P > 0.05$).

TABLE 3. COMPARISON OF THE DIETS (PERCENT BIOMASS BY SEED SPECIES), AMONG FIVE COEXISTING SPECIES (WHITE-CROWNED [WCSP], VESPER [VESP], SAVANNAH [SAVS], CHIPPING [CHSP], AND BREWER'S [BRSP] SPARROWS AT SITE 3 POOLED ACROSS MID- AND LATE-WINTER.

Seed species	Plant type[a]	Seed size[b]	WCSP	VESP	SAVS	CHSP	BRSP	$F_{4,265}$	P-value
Dropseed (*Sporobolus* spp.)	PG	0.1	15.89[d]	28.27[cd]	18.03[d]	20.72[cd]	45.18[c]	2.56	0.04
Threeawn (*Aristada* spp.)	PG-AG	0.5	0.0[d]	2.00[d]	1.24[d]	11.53[c]	8.29[cd]	4.19	0.01
Cupgrass (*Eriochloa* spp.)	AG	1.0	0.0[d]	0.72[d]	18.96[c]	0.41[d]	0.10[d]	10.99	0.01
Feather fingergrass (*Chloris virgata*)	AG	0.35	0.37[d]	12.74[c]	15.33[c]	19.27[c]	9.49[cd]	2.75	0.03
Stinkgrass (*Eragrostis cilianesis*)	AG	0.1	3.51[c]	1.76[c]	3.45[c]	3.73[c]	5.77[a]	1.25	0.29
Ammaranth (*Amaranthus* spp.)	FO	0.4	63.32[c]	24.47[c]	30.93[d]	10.30[e]	9.92[e]	16.73	0.01
Carpetweed (*Mollugo verticillata*)	FO	0.08	1.14[d]	3.90[d]	3.74[d]	15.72[c]	5.92[cd]	4.42	0.01
Other			15.77	26.14	8.32	18.32	15.33		

[a] PG = perennial grass, AG = annual grass, FO = forb.
[b] Size = Average seed weight (mg).
Note: Means with the same superscript within row did not differ significantly ($P > 0.05$).

other sparrow species. Savannah, Vesper, and Chipping Sparrows consumed more feather fingergrass seeds than White-crowned Sparrows. Consumption of stinkgrass did not differ among the five sparrow species. Consumption of amaranth differed significantly among sparrows with White-crowned Sparrows consuming significantly higher proportions than all other sparrow species; Savannah Sparrows consumed more amaranth seeds than Vesper, Chipping, and Brewer's Sparrows. Chipping Sparrows consumed significantly higher proportions of carpetweed seeds than Savannah, Vesper, and White-crowned sparrows.

COMPARING SOIL SEED BANK WITH SPARROW DIETS IN MID-WINTER

Comparisons of sparrow diets with soil seed banks in mid-winter were conducted in two ways: first by comparing sparrow diets with seed banks at a single site that supported the largest diversity of birds in mid-winter (Table 4) and secondly by comparing sparrow diets with seed banks across multiple sites, using a smaller sample of bird species that were found at multiple sites (Table 5). We present data on the most common and the most preferred seeds consumed; although not always the most preferred, the most common seeds comprised a substantial proportion of sparrow diets. Based on both percent biomass and ranked preference in sparrow diets, sparrows did not consume seeds in proportion to relative abundance (based on biomass) in the seed bank, but rather exhibited different degrees of seed preference (Tables 4 and 5). Preferred seeds were consumed at a substantially greater rate compared to availability, as measured by Johnson's rank preference.

At site 3, the only site where White-crowned Sparrow were found, amaranth and dropseed were both the preferred seeds and the most common seeds in the White-crowned Sparrow diet (Table 4). Chipping Sparrow exhibited a preference for dropseed, while carpetweed, feather fingergrass, and dropseed were the most common seeds in their diet. Brewer's Sparrow exhibited a preference for dropseed and stinkgrass, while dropseed was the most common seed in their diet (Table 4).

Savannah and Vesper Sparrows were the two most widely distributed species (each found at four of five sites) and exhibited varying patterns in diet composition across sites in mid-winter (Table 5). Cupgrass was the preferred seed of Savannah Sparrow at sites 1, 3, and 5 (Table 5). Cupgrass was not detected in the soil seed bank or Savannah Sparrow diets at

TABLE 4. COMPARISON OF THE DIETS (% BIOMASS AND PREFERRED RANK) OF MULTIPLE SPECIES WITH AVAILABLE SOIL SEED BANK (% BIOMASS) AT A SINGLE SITE (SITE 3) DURING MID-WINTER (JANUARY–MID-FEBRUARY 2003) USING JOHNSON'S RANK PREFERENCE (RANK). A BLANK SPACE MEANS THAT THE SEED SPECIES WAS NOT PRESENT AT THE SITE OR PROPORTIONS WERE <5% IN BOTH THE SOIL AND SPARROW DIETS.

	White-crowned Sparrow[a] (*Zonotrichia leucophrys*)			Chipping Sparrow[b] (*Spizella passerina*)			Brewer's Sparrow[c] (*Spizella breweri*)			Savannah Sparrow[d] (*Passerculus sandwichensis*)			Vesper Sparrow[e] (*Pooecetes gramineus*)		
Seed	Diet	Soil	Rank	Diet	Soil	Rank	Diet	Soil	Rank	Diet	Soil	Rank	Diet	Soil	Rank
Dropseed (*Sporobolus* spp.)	22.0	2.5	2.0^{f}	18.8	2.5	1.0^{f}	45.3	2.5	1.0^{f}	17.2	2.5	4^{g}	34.4	2.5	1.0^{f}
Threeawn (*Aristada* spp.)	0.0	7.6	5.0^{h}	12.8	7.6	4^{gh}	4.6	7.6	5.0^{h}	1.4	7.6	7.0^{j}	1.2	7.6	4.0^{i}
Cupgrass (*Eriochloa* spp.)										20.0	0.6	1.0^{f}			
Feather fingergrass (*Chloris virgata*)	0.3	13.9	6.0^{h}	19.5	13.9	5.0^{hi}	10.4	13.9	6.0^{h}	13.8	13.9	6.0^{i}	11.3	13.9	5.0^{i}
Stinkgrass (*Eragrostis cilianensis*)	5.0	2.5	3.0^{f}				8.8	2.5	2.0^{f}	7.6	2.5	2.0^{g}			
Amaranth (*Amaranthus* spp.)	53.2	5.5	1.0^{f}	1.3	5.5	2.0^{g}	5.1	5.5	3.0^{g}	26.5	5.5	3.0^{h}	15.2	5.5	2.0^{g}
Purslane (*Portulaca* spp.)	6.7	5.7	4.0^{g}	12.1	5.7	3.0^{gh}	9.2	5.7	4.0^{g}	5.1	5.7	5.0^{i}	9.3	5.7	3.0^{h}
Carpetweed (*Mollugo verticillata*)	2.2	34.7	7.0^{i}	26.2	34.7	6.0^{i}	8.7	34.7	7.0^{i}	6.0	34.7	8.0^{k}	6.8	34.7	6.0^{j}

[a] $F_{6, 38} = 298.98$, W = 1.80, P = 0.05.
[b] $F_{5, 10} = 11.09$, W = 2.19, P = 0.05.
[c] $F_{6, 20} = 94.40$, W = 1.88, P = 0.05.
[d] $F_{7, 60} = 270.89$, W = 1.77, P = 0.05.
[e] $F_{6, 26} = 344.70$, W = 1.84, P = 0.05.
Note: Seed species preferences that are ranked with the same superscript within a column (by bird species) did not differ significantly.

TABLE 5. Comparison of the diets (% biomass and preferred rank) of two broadly distributed species with soil seed bank (% biomass) at multiple sites during mid-winter (January–mid February 2003) using Johnson's rank preference (rank). Seed species ranked with the same superscript letter within a column (by bird species) did not differ significantly. A blank space means that the seed species was not present at the site or proportions were <5% in both the soil and sparrow diet.

Savannah Sparrow	Site 1^{a}			Site 3^{b}			Site 4^{c}			Site 5^{d}		
Seed	Diet	Soil	Rank	Diet	Soil	Rank	Diet	Soil	Rank	Diet	Soil	Rank
Dropseed (*Sporobolus* spp.)				17.2	2.5	4.0^{j}	2.7	6.4	3.0^{j}			
Threeawn (*Aristada* spp.)				1.4	7.6	7.0^{m}						
Cupgrass (*Eriochloa* spp.)	12.3	2.5	1.0^{i}	20.0	0.6	1.0^{i}				14.3	1.1	2.0^{i}
Feather fingergrass (*Chloris virgata*)				13.8	13.9	6.0^{l}	40.3	36.5	4.0^{k}			
Stinkgrass (*Eragrostis cilianensis*)	54.6	66.1	3.0^{j}	7.6	2.5	2.0^{j}	20.5	31.0	2.0^{j}	5.1	6.5	3.0^{j}
Amaranth (*Amaranthus* spp.)				26.5	5.5	3.0^{k}	16.7	1.2	1.0^{i}	41.1	6.1	1.0^{i}
Purslane (*Portulaca* spp.)				5.1	5.7	5.0^{l}						
Carpetweed (*Mollugo verticillata*)	11.6	4.3	2.0^{j}	6.0	34.7	8.0^{n}						
Vervain (*Verbena* spp.)	0.0	10.2	4.0^{k}									
Clover (*Trifolium* spp.)										0.0	17.9	
Neckweed (*Veronica peregrine*)										0.0	26.0	
Unidentified seed										0.0	16.9	

Vesper Sparrow	Site 1^{e}			Site 2^{f}				Site 3^{g}			Site 5^{h}		
Seed	Diet	Soil	Rank	Diet	Soil	Rank		Diet	Soil	Rank	Diet	Soil	Rank
Dropseed							34.4	2.5	1.0^{i}				
Threeawn								1.2	7.6	4.0^{l}			
Cupgrass	32.6	2.5	1.0^{i}	18.8	6.7	2.0^{j}							
Feather fingergrass				6.2	11.0	5.0^{kl}		11.3	13.9	5.0^{l}			
Stinkgrass	27.5	66.1	3.0^{i}	1.1	25.3	7.0^{m}					7.9	6.5	3.0^{j}
Amaranth				4.4	5.2	3.0^{j}		15.2	5.5	2.0^{j}	26.1	6.1	2.0^{i}
Purslane				1.9	10.9	4.0^{k}		9.3	5.7	3.0^{k}			
Carpetweed	16.2	4.3	2.0^{i}					6.8	34.7	6.0^{m}			
Vervain	0.0	10.2	4.0^{j}										
Clover											0.0	17.9	
Neckweed											0.0	26.0	
Goosefoot (*Chenipodium* spp)				12.9	0.6	1.0^{i}							
Panicum (*Panicum* spp.)				26.9	15.9	6.0^{l}							
Knotweed (*Polygonum* spp.)											13.9	1.1	1.0^{i}
Unidentified seed											0.0	16.9	

^{a} $F = 55.53_{3, 6}$, W = 2.32, P = 0.05.
^{b} $F = 270.89_{7, 60}$, W = 1.77, P = 0.05.
^{c} $F = 76.32_{3, 116}$, W = 1.75 , P = 0.05.
^{d} $F = 1232.99_{5, 49}$, W = 1.78, P = 0.05.
^{e} $F = 57.83_{3, 7}$, W = 2.21, P = 0.05.
^{f} $F = 344.70_{6, 26}$, W = 1.84, P = 0.05.
^{g} $F = 176.90_{5, 33}$, W = 1.81, P = 0.05.
^{h} $F = 70.47_{5, 31}$, W = 1.83, P = 0.05.
Note: Seed species ranked with the same superscript within a column (by bird species) did not differ significantly.

site 4; amaranth was the preferred seed type of Savannah Sparrow at this site. Amaranth was equally preferred by Savannah Sparrow at site 5 (Table 5). In comparison with seed preference, amaranth, feather fingergrass, and stinkgrass were variously the most common seeds in Savannah Sparrow diets (on a biomass basis) at different sites; only at site 5 did the most common seed coincide with a preferred seed type. Cupgrass was both the preferred and the most common seed species in the diets of Vesper Sparrow at site 1. Goosefoot (*Chenopodium* spp.) was preferred by Vesper Sparrow at site 2, while the most common seed in its diet was panicum. Dropseed was both the preferred and most common seed species in the diet at site 3. Knotweed and amaranth were preferred at site 5 where amaranth was the most common seed in Vesper Sparrow diets (Table 5). Seeds that were never consumed but were abundant in the soil included vervain (*Verbena* spp.), clover (*Trifolium* spp.), and neckweed (*Veronica peregrina*) (Table 5).

Seed Preference Among Sparrows for Mid- versus Late-Winter

Diets of four sparrow species (Chipping, Brewer's, Vesper and Savannah Sparrows) were compared in mid- and late-winter at site 3. Dropseed remained the preferred seed of three species (Chipping, Brewer's and Vesper Sparrows) in both mid- and late-winter; however, their preferences for other seed species changed between mid- and late-winter (Table 6). Amaranth was important for Chipping, Brewer's, and Vesper Sparrows in the mid-winter period but by late-winter was ranked lower (Table 6). Purslane remained relatively important for these same three species in both mid- and late-winter. Interestingly, threeawn ranked relatively low for the three species in mid-winter but was the second-most preferred seed species for Chipping and Brewer's Sparrows in late-winter; it was not found in the diet of Vesper Sparrow in late-winter (Table 6). Stinkgrass contributed less than 5% of Vesper and Chipping Sparrow diets in mid-winter but was relatively important in diets in late-winter.

Savannah Sparrow preferences changed substantially between mid- and late-winter. It was the only species to include the large-sized cupgrass seeds in its diet and it ranked as the preferred seed in mid-winter, followed by stinkgrass and amaranth. In late-winter, Savannah Sparrow preference switched to the small-sized dropseed, followed by purslane and feather fingergrass.

TABLE 6. Comparison of diet preferences in mid- and late-winter for four sparrows at site 3 using Johnson's preference rank. Statistics for mid-winter are found in table 4.

Seed	Chipping Sparrow[a] (*Spizella passerina*)		Brewer's Sparrow[b] (*Spizella breweri*)		Savannah Sparrow[c] (*Passerculus sandwichensis*)		Vesper Sparrow[d] (*Pooecetes gramineus*)	
	Mid-winter Rank	Late-winter Rank	Mid-winter Rank	Late-winter Rank	Mid-winter Rank	Late-winter Rank	Mid-winter Rank	Late-winter Rank
Dropseed (*Sporobolus* spp.)	1.0[ae]	1.0[e]	1.0[e]	1.0[e]	4.0[h]	1.0[e]	1.0[e]	1.0[e]
Threeawn (*Aristada* spp)	4.0[fg]	2.0[f]	5.0[g]	2.0[f]	7.0[j]		4.0[h]	
Cupgrass (*Eriochoa* spp.)					1.0[e]			
Feather fingergrass (*Chloris virgata*)	5.0[gh]	5.0[h]	6.0[g]	5.0[h]	6.0[i]	3.0[fg]	5.0[h]	5.0[g]
Stinkgrass (*Eragrostis cilianensis*)		4.0[h]	2.0[e]	4.0[h]	2.0[k]	5.0[g]		3.0[fg]
Amaranth (*Amaranthus* spp.)	2.0[f]	7.0[i]	3.0[f]	6.0[i]	3.0[k]	4.0[fg]	2.0[f]	4.0[g]
Purslane (*Portulaca* spp.)	3.0[fg]	3.0[g]	4.0[f]	3.0[g]	5.0[i]	2.0[f]	3.0[g]	2.0[f]
Carpetweed (*Mollugo verticillata*)	6.0[h]	6.0[i]	7.0[h]	7.0[i]	8.0[k]	6.0[h]	6.0[i]	6.0[h]

[a] $F = 77.17_{6, 35}$, $W = 1.81$, $P = 0.05$)
[b] $F = 78.75_{6, 6}$, $W = 2.24$, $P = 0.05$)
[c] $F = 37.93_{5, 7}$, $W = 2.18$, $P = 0.05$)
[d] $F = 32.70_{5, 10}$, $W = 2.04$, $P = 0.05$)
Note: Seed species ranked with the same superscript within a column (by bird species) did not differ significantly.

DISCUSSION

Seed production varied substantially across our five study sites (41.2–141.5 kg/ha) and was similar to or higher than reported seed production in southeast Arizona, which was found to be low (7.4–44.2 kg/ha) during years of below normal precipitation (Pulliam and Dunning 1987), and to vary widely (0.2–88.9 kg/ha) in relation to summer precipitation (Pulliam 1986). The higher production at some of our sites was likely related to the slightly disturbed nature of some sites (vicinity of cattle watering areas). Similar to Pulliam (1986), we observed a substantial decline in seed availability from mid- to late-winter, suggesting that winter sparrows and possibly other granivores consumed large quantities of seed.

In general, diets of sparrows and the soil seed bank samples at our sites were diverse. In many cases, the preferred seeds (dropseed, cupgrass, amaranth, goosefoot, knotweed, and carpetweed) were not the most abundant in sparrow diets or the soil seed bank. In a few cases the dominant seeds in the soil seed bank samples were also the most common but not preferred in sparrow diets (stinkgrass at site 1 for Savannah Sparrow and perhaps Vesper Sparrow, carpetweed at site 3 for Chipping Sparrow, and featherfinger grass at site 4 for Savannah Sparrow). Threeawn only appeared important in late winter after substantial declines in available seed biomass.

With the exception of the perennial dropseed, panicum, and threeawn species, sparrow diets consisted of annual grass and forb seeds (panicum and threeawn species can be perennial or annual depending on the species). This may reflect the slightly disturbed nature of our study sites. However, these results are similar to Pulliam's findings (1980, 1986) that annual grass and forb seeds were dominant in Chipping Sparrow diets in southeast Arizona, even though several perennial grass species were also present. Forb seeds tend to be unarmored (lacking the awns of many grass species), making it easy for sparrows to consume these seeds without husking. Forbs also tend to produce many seeds that fall in clumps in the immediate vicinity of the plant (Brown et al. 1979). High densities of forbs may result in a clumped distribution and high abundance of seeds that allow sparrows to quickly consume large quantities to meet their energy requirements. Annual grasses also produce large quantities of seed as do perennial grasses in the genus *Sporobolus* (dropseed grasses). Dropseed was apparently not available on Pulliam's (1980, 1986) study site. However, the similarly small-sized Lehmann lovegrass, an exotic perennial that also produces numerous seeds, was the dominant perennial grass seed and important in Chipping Sparrow diets in Pulliam's study.

Some seed species present in the soil seed bank were never detected in avian diets, suggesting that sparrows avoided, or at the very least did not prefer, certain seed species. For example, vervain (*Verbena* spp.) was relatively abundant in the soil seed bank at site 1 and neckweed (*Veronica peregrina*) and clover were abundant in the soil seed bank at site 5, yet these species were never detected in avian diets. Pulliam (1980) also observed this for Chipping Sparrow in southeast Arizona. Avoidance of abundant seed suggests that other factors such as toxicity (Sherbrooke 1974, Pulliam 1980, Henderson 1990), nutrient content (Glück 1985, Greig-Smith and Wilson 1985, Diaz 1989), accessibility, seed coating, and digestibility (Greig-Smith and Crocker 1986) may influence seed preferences.

In southeast Arizona, interspecific competition among sparrow species has been found to affect resource selection (Pulliam 1975, Pulliam and Mills 1977, Pulliam 1986). There is evidence in our results to suggest that sparrows partitioned seed resources at the site where we caught the greatest number of species. This site had the combination of a high abundance and an intermediate diversity of seeds. We observed substantial differences in seeds present in the diets of sparrows captured at this site and seeds were not consumed in relation to availability. White-crowned and Brewer's Sparrows had a narrower diet than other species. White-crowned Sparrow exploited amaranth seeds (63% of their diet), a medium sized forb seed that was relatively large, and swallowed whole (no husking required). Brewer's Sparrows specialized on dropseed (45% of diet), a small, unarmored grass seed. The apparent narrower diet, however, may be due, in part, to the smaller sample sizes for these two species compared to the other three dominant sparrows.

Pulliam (1986) argued that sparrow species should have less dietary overlap when seed production is high. In years of high seed production, such as the year of our study, he suggested little or no overlap will occur among co-existing species because sparrows will specialize on seeds they consume the most efficiently. Based on seed biomass and handling time, Pulliam (1985) predicted smaller sparrows should specialize on smaller seeds and larger sparrows on larger seed sizes. However, he suggested that large bodied sparrows should be equally efficient at handling small and large-sized seeds whereas small bodied sparrows would be most efficient at handling small-sized seeds. We observed the two small-bodied sparrows (Chipping and Brewer's Sparrows) to exhibit a preference for the small-sized seeds supporting Pulliam's assertion that small-bodied sparrows specialize on small-sized seeds when seed production is intermediate to high. However, our observations related to the diets of the larger-bodied sparrows did not follow Pulliam's theory; seed preferences varied among the three larger-bodied sparrows from large- to small-sized seeds. Benkman and Pulliam (1988) suggested resource partitioning is less pronounced in emberizid sparrows because they consume a smaller range of seed sizes and these seeds have fewer structural defenses. The observed variability in seed size preferences by the larger-bodied sparrows in our study suggests that seed size and availability are not the only factors driving seed selection by larger-bodied sparrows. The observed variability in the diets of Savannah and Vesper sparrows across sites supports the assertion that larger-bodied sparrows can efficiently consume a greater variety of seed sizes. This was especially evident for the larger Vesper Sparrow that had a different preferred seed at each of the four sites where it was present, with preferred seed sizes ranging from 0.1 to 1.8 mg.

Changes in seed preferences are likely related to changes in the relative abundance of seeds throughout the winter and due to changes in avian community composition. We observed a shift in seed preferences by sparrows from mid- to late-winter at site 3 where seed biomass declined by 50% over the same time period and the relative abundance of seed species changed. Dropseed remained the preferred seed species for sparrows in mid- and late-winter with the exception of Savannah Sparrow. This seed species had a slight increase in relative abundance in late-winter compared to mid-winter, and this seed species increased in Chipping and Brewer Sparrows diets in late winter. The larger, armored threeawn seeds also became substantially more important in the diets of both sparrows despite a substantial decline in relative abundance (7.6% vs 0.7%) between mid- and late-winter, respectively. The small stinkgrass seed was not consumed by Chipping Sparrow in mid-winter but was part of their diet in late winter likely because this seed species had a higher relative abundance in late-winter. Diets changed substantially for Savannah Sparrow between the two winter periods whereas Vesper Sparrow diets changed somewhat but dropseed remained the preferred seed species during both periods. The large-sized cupgrass was preferred by Savannah Sparrows in mid-winter; however, cupgrass had almost disappeared from the soil seed bank samples by late-winter. In response, it also disappeared from Savannah Sparrow diets and was replaced by the smaller sized dropseed. Pulliam (1980, 1986) also observed a shift in diet for Chipping Sparrow from mid- to late-winter with a diet shift toward larger, armored seeds. We did not observe a clear dietary shift in any of the dominant species. Chipping and Brewer's Sparrows, however, did consume substantially more of the large-sized, armored threeawn seeds in late winter but their diet included a diversity of seed sizes and types during both winter periods.

Winter sparrows consumed a large diversity of seed throughout the winter period. Perennial and annual grasses and forb seeds were all important components of sparrow diets. The dominance of a few key seed species in the diets of all winter sparrow species has strong implications for the management of granivorous birds and associated habitats in the southwestern United States and northern Mexico. Dropseed seeds were important in the diets of all five sparrow species. Based on our study, results indicate that seeds from dropseed are an important component of winter sparrow diets. This is an abundant perennial grass species in the Chihuahuan Desert and management of grasslands with a large dropseed component may influence seed production and distribution. Proper grassland management during the growing season is critical to ensure sufficient seed production for granivorous sparrows. Additional data are needed on the effects of the timing and intensity of livestock grazing and other management practices on seed production in grasslands containing dropseed species.

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