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DIET OF NESTING SAVANNAH SPARROWS IN INTERIOR ALASKA

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Abstract.—Grasshopper populations on the Delta Agriculture Project area in interior Alaska exhibit a strong biennial periodicity (>25/m^2 in one year and <1/m^2 in the next). Savannah Sparrow (*Passerculus sandwichensis*) stomach contents were examined during the breeding seasons over a 3-yr period. Grasshoppers constituted the largest portion (>45%) of the diet of adult Savannah Sparrows in the high grasshopper years of 1990 and 1992. Beetles and hemipterans comprised the majority (66.5%) of their food in the low grasshopper year of 1991. Grasshopper presence in the diet varied in individual birds and among years. Occurrence in the diet of other arthropod taxa was independent of year, but varied among individuals. Almost no utilization of plant material was recorded. The results illustrate the responsiveness of breeding birds to a variable food supply and preference for highly nutritious grasshoppers when they are available.

DIETA DE *PASSERCULUS SANDWICHENSIS* ANIDANDO EN EL INTERIOR DE ALASKA

Sinopsis.—Poblaciones de saltamontes en el área del Proyecto de Agricultura del Delta en el interior de Alaska exhiben una fuerte periodicidad anual (>25/m^2 en un año y <1/m^2 en el próximo). Estómagos de individuos de *Passerculus sandwichensis* se examinaron a través de 3 años durante las temporadas reproductivas. Los saltamontes constituyeron la mayor parte (>45%) de la dieta de estas aves en los años de 1990 y 1992, cuando los saltamontes abundaron. Escarabajos y hemipteros formaron la mayor parte de la dieta en el año de 1991, donde los saltamontes escasearon. La presencia de saltamontes en la dieta de las aves varió entre individuos y a través de los años de estudio. La presencia de otros taxones de artrópodos en la dieta fué independiente del año, pero varió entre individuos. Casi no se registró el uso de material vegetal en la dieta de las aves. Los resultados ilustran la respuesta de aves anidantes a una fuente variable de alimento como también la preferencia por alimentos altamente nutritivos como los saltamontes cuando el mismo está accesible.

During the breeding season, granivorous/omnivorous birds commonly switch to an animal (primarily insect) diet in response to increased demands for protein, energy, and other nutrients that result from reproductive activities (Jones and Ward 1976, Robbins 1981, West 1973, Williams 1987). For many avian species grasshoppers are an important component of the breeding-season diet (Martin et al. 1951) due to their high crude protein content (>50%), energy value, and other nutrients (DeFoliart 1975, Ueckert et al. 1972). Availability is also a major factor influencing usage and appearance of food items in the diet (Krementz and Ankney 1988, Twedt et al. 1991). We investigated which animal foods were important to nesting Savannah Sparrows (*Passerculus sandwichensis*), and particularly, the dietary response to a unique biennially fluctuating grasshopper population.

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METHODS

The study was conducted during the summers (25 May–25 July) of 1990, 1992 (high grasshopper years) and 1991 (low grasshopper year) on the Delta Agriculture Project, Alaska, an approximately 44,500-ha area located south of the Tanana River, and extending approximately 150 km east of Delta Junction, Alaska (64°00′N, 145°20′W). The project began in the late 1970s for the purpose of farming small grains and hay. The project area is a mosaic of different-aged fields cleared from the surrounding forest of black spruce (*Picea mariana*), white spruce (*P. glauca*) and aspen (*Populous tremuloides*). Cereals (mainly barley), grass seed, and hay are the primary crops grown in the area. Approximately 20% (8900 ha) of the available land is currently in production. The remainder (35,600 ha) is idle or in government set-aside programs. The idle and set-aside sites are comprised of a variety of grasses (*Calamagrostis* spp., *Agropyron* spp., *Festuca* spp.) and forbs (*Epilobium* spp.), interspersed with willow (*Salix* spp.) and aspen windrows.

As part of a larger research project investigating the effects of range grasshopper control programs on non-target wildlife, adult Savannah Sparrows were collected throughout the agriculture project at random locations and random times during the day. Collections were made when the majority (>50%) of the Savannah Sparrows were caring for nestlings. Birds were collected using a 20-gauge shotgun and specimens were placed on ice within 1 h of collection (U.S. Fish and Wildlife Service permit # PRT-750470, Alaska state permit # 92-55). Specimens were kept frozen at −80 C in the laboratory until thawed for examination. The esophagus and gizzard were removed and contents flushed with 70% Ethyl Alcohol into a petri-dish. The contents were sorted to remove identifiable and unidentifiable arthropod and plant parts.

We used various sources to aid in identification of the arthropod parts (Borror et al. 1981, Calver and Wooller 1982, Chapman and Rosenberg 1991, Moreby 1988, Ralph et al. 1985). Individual arthropods within a sample could be identified and counted on the basis of parts available (e.g., six beetle legs = one Coleoptera, two spider fangs or chelicera = one Arachnida, two grasshopper mandibles = one Orthoptera). Odd numbers of parts were counted as an additional individual. As plant material was seldom encountered, plant contents were visually estimated as a percentage of total sample, and not identified.

We used a multi-way contingency table to separate effects of year, sex and individual birds on use of arthropod taxa (PROC CATMOD, SAS Institute, Inc. 1988:189–282). Responses were measured by the number of individual arthropods in a taxon within a gut.

Grasshopper abundance was indexed two ways. First, contents of 40 passes of a 0.4-m diameter insect net were collected in a 5-m radius around transect poles (set approximately 90 m apart) at six selected sites representative of the grassland vegetation. Transects varied in length (538–956 m); however, we collected a minimum of six sweep samples on

TABLE 1. Diet ($\bar{x} \pm 1$ SE individuals per gut and percent of total gut contents in parentheses) of Savannah Sparrows during high (1990, 1992) and a low (1991) grasshopper years in Alaska.

Order	1990	1991	1992
Orthoptera	7.50 ± 0.72 (45.8)	1.08 ± 0.52 (8.2)	11.6 ± 1.82 (56.2)
Hemiptera	0.31 ± 0.23 (1.9)	2.38 ± 1.20 (18.0)	1.68 ± 1.18 (8.1)
Homoptera	0.86 ± 0.53 (5.2)	0.88 ± 0.53 (6.6)	1.52 ± 0.46 (7.4)
Coleoptera			
Adult	2.42 ± 0.40 (14.7)	6.29 ± 1.14 (47.6)	3.56 ± 0.65 (17.2)
Larvae	2.38 ± 1.57 (14.5)	0.13 ± 0.09 (0.9)	0.12 ± 0.12 (0.6)
Lepidoptera			
Adult	0.04 ± 0.04 (0.2)	0.00 ± 0.00 (0.0)	0.04 ± 0.04 (0.2)
Larvae	0.38 ± 0.15 (2.3)	0.17 ± 0.08 (1.3)	0.52 ± 0.14 (2.5)
Diptera	0.23 ± 0.16 (1.4)	0.17 ± 0.13 (1.3)	0.08 ± 0.06 (0.4)
Hymenoptera	0.04 ± 0.04 (0.2)	1.08 ± 0.88 (8.2)	0.00 ± 0.00 (0.0)
Arachnidae	2.27 ± 0.34 (13.8)	1.04 ± 0.27 (7.9)	0.96 ± 0.14 (4.7)
Mollusk	0.00 ± 0.00 (0.0)	0.00 ± 0.00 (0.0)	0.56 ± 0.56 (2.7)

each transect. Samples were collected between 1000 and 1200 hours Alaska Standard Time. Collections were made once during the nestling stage (approximately 12–24 June) each year. Grasshoppers were separated from all other arthropods, dried at 100 C in an oven for 48 h, then weighed to the nearest 0.0001 g. The other arthropods collected were dried and weighed in the same manner. No attempt was made to separate arthropods, other than grasshoppers, into taxonomic categories. Mean biomass was determined by taking the total mass of 40 sweeps at each transect pole and averaging those to obtain an estimate for each site. Mean biomass per year was determined by averaging the means for the six sites.

Second, we estimated grasshopper densities using circular aluminum rings (Onsager and Henry 1977). At each of three sites 40 0.1-m^2 rings were positioned in four rows of 10 placed 5 m apart. We counted the number of grasshoppers within each ring as they flushed in response to our approach; vegetation within each ring was brushed to flush any remaining grasshoppers. Grasshoppers were counted weekly in 1990, once every 3 wk in 1991, and once every 2 wk in 1992. The number of grasshoppers in each ring was summed for each row then averaged for the four rows to obtain a density estimate for the grid. Ring counts and sweep samples were taken only when temperatures where >19 C and wind velocity was <10 km/h.

We analyzed the density and biomass data using a General Linear Model format. Then we performed a Tukey's Multiple-comparison test to identify differences among years (SAS Institute, Inc. 1988:549–640).

RESULTS

We collected a total of 75 birds (26 [20 males, 6 females] in 1990, 24 [15 males, 9 females] in 1991, and 25 [18 males, 7 females] in 1992).

TABLE 2. Biomass[a] (g, $\bar{x} \pm 1$ SE) of grasshoppers and other arthropods during high (1990, 1992) and low (1991) grasshopper years on the Delta Agriculture Project, Alaska.

Arthropod	1990	1991	1992
Grasshoppers	1.23 ± 0.19	0.003 ± 0.009	0.03 ± 0.009
Other	0.09 ± 0.01	0.05 ± 0.002	0.09 ± 0.007

[a] Dry mass biomass per 40 sweeps of a 0.4-m diameter insect net in a 5-m radius circle.

Diet composition is summarized in Table 1. There were statistically significant differences among years in the use of grasshoppers ($\chi^2 = 67.93$, $P < 0.0001$, df = 2). There were no differences between males and females in use of grasshoppers ($\chi^2 = 0.02$, $P = 0.90$, df = 1). There were, however, highly significant differences in grasshopper use among individual birds across years and sex ($\chi^2 = 314.00$, $P < 0.0001$, df = 69). There was considerable among bird variation in the number of grasshoppers found within a gut regardless of sex or year. In contrast to this relationship, none of the other taxa (Hemiptera, Homoptera, Coleoptera, etc.) differed significantly ($P > 0.05$) between years or sexes. Among-bird variation was significantly ($P < 0.0001$) different for all the taxonomic categories, however.

Overall, less than 5% of each sample contained seeds or leaves. Grit was found in only a few samples also indicating a low use of plant material in the diet (Bird and Smith 1964).

Ring counts indicated that grasshopper densities were greatest in 1990 and 1992 (60.9 ± 10.6 grasshoppers/m^2 in 1990, 0.4 ± 0.2 grasshoppers/m^2 in 1991, and 9.7 ± 4.4 grasshoppers/m^2 in 1992). Densities in 1990 were greater than in 1991 and 1992 ($F_{[2,45]} = 21.96$, $P = 0.0001$; Tukey's multiple-comparison test). Densities in 1992, however, were not significantly greater than in 1991 ($P > 0.05$). Sweepnet samples are summarized in Table 2. Grasshopper biomass in 1990 was greater than 1991 and 1992, and 1992 biomass was greater than 1991 ($F_{[2,15]} = 41.12$, $P = 0.0001$; Tukey's multiple-comparison test). Biomass of other arthropod taxa collected was lower in 1991 than in either 1990 or 1992 ($F_{[2,15]} = 15.97$, $P = 0.0002$; Tukey's multiple-comparison test), but 1990 did not differ from 1992. Field methodology and sampling variation may have contributed to discrepancies between ring counts (84% lower in 1992 than 1990) and grasshopper biomass (98% lower) in measuring differences among years.

DISCUSSION

Savannah Sparrows are primarily granivorous during the non-breeding season (Bent 1968) and are known for their wide geographic distribution and diverse diet (Judd 1901, Meunier and Bédard 1984, Wheelwright and Rising 1993). The variety of arthropods utilized and the nearly 100% animal matter in the diet in our study is consistent with other studies indicating that nearly all small land birds switch to protein-rich animal diets during the breeding season especially for feeding their young (Bird and Smith 1964, Martin et al. 1951, West 1973). Food items selected within a year and among years probably reflect the relative abundance and availability of those items in the local environment which is particularly true of grasshoppers in our study during the high density years. Occurrence in the diet of arthropod taxa varied more among individual Savannah Sparrows than among years or between sexes (other than the year-effect for grasshoppers) which suggests individual Savannah Sparrows exhibit some degree of plasticity even when a particular prey item (grasshoppers) is conspicuously abundant, although it may simply reflect local grasshopper availability within the bird's foraging area. Differences in diet among years has also been demonstrated for shrubsteppe birds (Rotenberry 1980).

The most common grasshopper species (*Melanoplus sanguinipes*) in the study area requires 2 yr to complete its life cycle at this northern latitude (United States Department of Agriculture 1992) and the peak-hatch years are synchronized. This phenomenon explains the biennial periodicity of their abundance (Miller 1993). During the low grasshopper year, however, when densities of grasshoppers were $< 1/m^2$, grasshoppers still made up 8% of the diet. The ability of Savannah Sparrows to locate and capture grasshoppers during periods of relatively low availability has important implications for the role of birds in regulating grasshopper populations and preventing or dampening outbreaks (Bock et al. 1992, Fowler et al. 1991, McEwen 1987). Predation on low density populations has much greater regulating potential than when prey numbers are high (Krebs 1985).

Studies involving experimental manipulations of food supplies have increased the understanding of functional, reproductive and numerical responses in birds (Boutin 1990, Martin 1987, Rodenhouse and Holmes 1992). Our study demonstrates the high degree of dietary adaptability in a population of nesting Savannah Sparrows in response to a naturally fluctuating arthropod food base. Similar dietary plasticity has been demonstrated in other passerines among years (Rotenberry 1980) and during cyclical arthropod outbreaks (Buckner and Turnock 1965, MacArthur 1958). Further study of the Alaska grasshopper-bird relationships would provide longer-term data on the plasticity of the Savannah Sparrow population and could include response of other avian species to the extreme changes in the food resource.

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