

RESPONSES OF NESTING SAVANNAH SPARROWS TO FLUCTUATIONS IN GRASSHOPPER DENSITIES IN INTERIOR ALASKA

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ABSTRACT.—Grasshopper populations on the Delta Agricultural Project area in interior Alaska exhibit a strong biennial periodicity. This phenomenon allowed us to study dietary, reproductive, and numerical responses of nesting Savannah Sparrows (*Passerculus sandwichensis*) to fluctuations in prey abundance. Grasshopper densities exceeded 25/m² in 1990 but were less than 1/m² in 1991. In 1990, 61% of the identifiable food items brought to the nest were grasshoppers. In 1991, Lepidoptera larvae and Diptera were the most common items brought to the nests and no grasshopper deliveries were observed. Fledging success was 97% in 1990 and 96% in 1991. At least one nestling per nest successfully fledged each year. Mean clutch size was significantly higher during the high grasshopper densities in 1990. Reduced growth measurements of nestlings were obtained in 1991 compared to 1990. Effects on growth appeared to be greater early in development, rather than prior to fledging. Savannah Sparrow densities did not differ between the two years. Although a positive response to high grasshopper densities was observed, the magnitude of the response was diminutive compared with the large difference in prey abundance between years. This suggests that factors other than food limit reproductive output in this population of Savannah Sparrows. Received 13 May 1993, accepted 2 July 1993.

PREDATORS EXHIBIT CHANGES in reproduction, diet, and density in response to changes in prey density. Numerical responses often take the form of a density-dependent relationship of a predator corresponding to changes in prey density. Predators also respond to changes in prey abundance by switching their diet (Solomon 1949). Modifications in clutch size and changes in survival or growth rates of nestlings indicate a reproductive response. Lack (1947, 1954) developed a theoretical model relating food abundance to reproductive success in bird populations. Since then a number of studies have examined whether reproductive success can be altered by manipulating food abundance (Murphy and Haukioja 1986, Martin 1987, Boutin 1990, Simons and Martin 1990). Many authors have documented the response of birds (particularly Passeriformes) to natural changes in food availability (e.g. Zach and Falls 1975, Anderson 1977, Sealy 1980, Marr and Raitt 1983, Strehl and White 1986).

In the interior of Alaska, grasshopper populations (predominantly *Melanoplus sanguinipes*) fluctuate biennially with populations during high years reaching densities of more than 25/m²; densities in low years are less than 1/m² (1990 U.S. Dep. Agriculture internal report by Sluss and Franklin). This natural biennial fluctuation allowed us to investigate whether nesting Savannah Sparrows (*Passerculus sandwichensis*) showed dietary, reproductive, and numerical responses during two breeding seasons, one with high grasshopper numbers and one with low grasshopper numbers. We anticipated a switch from grasshoppers in the high grasshopper year of 1990 to alternative foods in the low grasshopper year of 1991. In addition, we expected a between-year reduction in feeding rates to nestlings as the grasshoppers became unavailable. We predicted Savannah Sparrows would show a positive reproductive response to high grasshopper numbers in 1990 by increasing clutch size, producing larger nestlings and fledging more nestlings per nest than in the low grasshopper year of 1991. Finally, we anticipated a change in adult Savannah Sparrow density either through immigration into

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the 1990 breeding population or recruitment into the 1991 population.

METHODS

Our study was conducted during the summers (25 May–25 July) of 1990 (high grasshopper year) and 1991 (low grasshopper year) on the Delta Agriculture Project, Alaska. The Delta Agriculture Project, covering approximately 44,500 ha south of the Tanana River, extends for approximately 150 km east of Delta Junction, Alaska (64°00'N, 145°20'W). The entire agriculture project is surrounded by spruce forest, making this population of Savannah Sparrows relatively isolated from other Savannah Sparrow populations in the region. The Delta Agriculture Project was begun in the late 1970s for farming small grains, and it is a mosaic of different-aged fields cleared from the surrounding forest of black spruce (*Picea mariana*), white spruce (*P. glauca*), and aspen (*Populus tremuloides*). Cereals (mainly barley), grass seed, and grass hay are the primary crops grown in the area. Approximately 20% (8,900 ha) of the available land is currently in production. The remainder is idle or in government set-aside programs.

Two sites, each comprising approximately 150 ha, were selected for study. Vegetation of both sites consisted of grasses (*Calamagrostis* spp., *Agropyron* spp., *Festuca* spp.) and forbs (*Epilobium* spp.), interspersed with willow (*Salix* spp.) and aspen windrows.

Savannah Sparrow nests were located by dragging a heavy rope over the grass and flushing adults from nests. To facilitate relocating nests, a small flag on a 0.5-m-high wire was placed 5 m north of each nest. Nests were visited daily until the first egg hatched (day 0), and then revisited four and seven days later. Individual nestlings were marked with Liquid Paper on their claws for later identification. A clutch was considered complete if the clutch size was unchanged for two consecutive visits. Hatching success was calculated as the number of unhatched eggs in the nest on day four divided by the complete clutch size. At each posthatch visit the number of nestlings and unhatched eggs were recorded and growth parameters were measured. Nestling mass was measured to the nearest 0.1 g using a 30-g Pesola spring scale suspended in a transparent cylindrical plastic tube to minimize wind disturbance. Tarsus length and length of the ninth primary were measured for all nestlings to the nearest 0.01 mm using dial calipers. Mean growth rates for broods were calculated by subtracting the mean value of each growth variable (ninth primary, tarsus, and mass) on day 4 from the mean value of each variable on day 7, and then dividing by the number of minutes that elapsed between measurements. This value was then converted to amount gained per day. Only nests discovered before hatching were used in analyses. A nest was considered successful if at least one nestling fledged from it. The

number of nestlings remaining in the nest on the second visit (day 7) was assumed to be the number of birds that successfully fledged. Nestlings typically fledged on day 8 or 9. Fledging success (percent of nestlings surviving until fledging) was determined by dividing the number of nestlings on day 7 by the number of nestlings on day 4. Blowfly larvae (*Protophthora* spp.) were found in nestlings at 14 nests (4 [15% of all nests] in 1990 and 10 [30%] in 1991). Parasitized nestlings had reduced growth rates and were not included in the growth analyses (C. K. Miller unpubl. data).

Dietary information was collected at 11 nests in each of the two years. Blinds were erected 5 to 7 m from each nest on day 3 posthatch, and observations were made on day 4 posthatch. Each nest was viewed continuously for 2.0 to 2.5 h following the first feeding visit after the observer entered the blind. We monitored 21 of the 22 nests during the first half of the daylight cycle (0400 to 1200 Alaska Standard Time [AST]). Feeding rate did not change with time of day in a population of Savannah Sparrows in Nova Scotia (Stobo and McLaren 1975). Prey were identified to major taxa with the aid of binoculars and a spotting scope. This technique probably biased samples towards large arthropods. The length of foraging bouts was determined by dividing the amount of time spent away from the nest by the number of feeding trips made to the nest during the observation period.

Birds were censused using a line-transect method (Emlen 1977). Three line transects of variable length (range 538–956 m) were established on each site (lengths totaled 2,079 m at one site and 2,505 m at the other). Flags were placed parallel to the transect route at 25 and 50 m to aid in estimating the distance of birds from the transect center. The same transects were used each year and run once when the nests contained nestlings (62% in 1990, 50% in 1991) or eggs. Transects were run during the morning activity period of the birds (0400–0800). The perpendicular distance from the line to each bird detection, and the manner in which the bird was detected (visual, singing, calling, both visual and auditory), were recorded as the observer slowly walked the transect (ca. 1.5 km/h).

Grasshopper abundance was indexed in two ways. First, at each pole marking the line transects (poles were approximately 90 m apart), contents of 40 passes of a 0.4-m diameter sweep net swept in a 5-m radius were collected between 1000 and 1200. Collections were made during: (a) incubation stage (late May to 12 June); (b) nestling stage (13–24 June); and (c) fledging stage (>24 June). Grasshoppers were separated from all other arthropods, dried at 100°C in an oven for 48 h, and weighed to the nearest 0.0001 g. The other arthropods collected were dried and weighed in the same manner. Mean biomass per nesting stage was determined by taking the total mass of 40 sweeps at each line-transect pole and averaging those to ob-

TABLE 1. Biomass* (g; $\bar{x} \pm \text{SE}$) of grasshoppers and other arthropods during high (1990) and low (1991) grasshopper years on the Delta Agriculture Project, Alaska, with results of Kruskal-Wallis test.

	1990	1991	H	P
Grasshoppers	1.37 \pm 0.20	0.003 \pm 0.002	26.4	0.0001
Other arthropods	0.18 \pm 0.03	0.075 \pm 0.013	12.3	0.0004

* Dry-weight biomass per 40 sweeps of a 0.4-m radius insect net within a 5-m radius circle.

tain an estimate for each transect. Mean biomass per year was estimated by averaging the means for the three stages.

Second, we estimated grasshopper densities using circular aluminum rings (Onsager and Henry 1977). At each of two sites, 40 0.1-m² rings were positioned in four rows of 10 placed 5 m apart. Each grid was placed in the same habitat. One grid was less than 1 km from one study site, while the other was 5 km from the second study site. We counted the number of grasshoppers within each ring as they flushed to our approach; vegetation within each ring was brushed to flush any remaining grasshoppers. Grasshoppers were counted weekly in 1990 beginning in late May and continuing into mid-July, and once every three weeks in 1991 beginning in early June and continuing until late July. After the number of grasshoppers in each ring was summed for each row, the four rows were averaged to obtain a density estimate for the grid. Ring counts were made only when temperatures were greater than 19°C and wind velocity was less than 10 km/h.

Statistical analysis.—Because microhabitat and food-supply differences may exist between sites (Quinney et al. 1986), we tested for differences between sites within years. However, we found no differences in any of the parameters, including grasshopper and other arthropod biomass. Therefore, we pooled the information from both sites within each year. Normality of the data was tested using a Shapiro-Wilk statistic (Shapiro and Wilk 1965). Clutch size and number of birds fledged per nest were analyzed using a G-test (Sokal and Rohlf 1981:696–721). Hatching success, fledging success, arthropod biomass, grasshopper biomass, and grasshopper density were analyzed using a Kruskal-Wallis (KW) test (Sokal and Rohlf 1981:429–432). Growth data, feeding rates, length of foraging bouts, and amount of time spent brooding were analyzed using a generalized linear model (GLM; SAS Institute 1988:549–640). Differences in the amounts of each taxon fed to nestlings between years were analyzed using *t*-tests. Differences in the variety of taxa fed to nestlings between years were analyzed using a Wilcoxon rank-sum statistic. Sparrow densities were estimated using the program DISTANCE (Buckland et al. 1993). Observations were truncated at 90 m on each side of the line. Transect data were fit to a hazard function (Buckland 1985), and the difference in density estimates was analyzed using a *t*-test. Statistical significance was set at the 0.05 probability level.

RESULTS

Nesting phenology and grasshopper development.—Savannah Sparrow nesting phenology was similar between years. The median date for clutch initiation (first egg day) was 31 May 1990 ($n = 23$) and 29 May 1991 ($n = 42$); median hatching dates were 17 June 1990 and 15 June 1991; median fledging dates were 25 June 1990 and 23 June 1991. More than 52% of clutches were initiated within a three-day (one day before through one after median) period in 1990, and more than 42% of clutches were within the three-day period in 1991.

A unique feature of Alaskan grasshopper development is a prolonged hatch, which continues over 30 days. This is primarily due to microhabitat temperature differences (1990 U.S. Dep. Agriculture internal report by Sluss and Franklin). The first nymphal stages of grasshoppers were observed as early as 21 May 1990. Second and third nymphal stages were present by 30 May. Full adult stages were seen by 20 June. Grasshoppers were rarely seen in 1991 so their phenology was unknown.

Grasshopper biomass and density estimates.—Grasshoppers were much more abundant in 1990 than in 1991 as indicated in both sweep-net samples (Table 1) and ring counts. Overall grasshopper densities between years from ring counts averaged 66.4 \pm SE of 12.1 grasshoppers/m² in 1990 and 0.3 \pm 0.2 grasshoppers/m² in 1991 ($H_1 = 12.20$, $P < 0.001$; KW test). Other arthropods also were more abundant in 1990 than in 1991 (Table 1). There were no between-site differences in grasshopper or other arthropod biomass within years (1990, $F_{4,31} = 0.21$, $P = 0.65$; 1991, $F_{4,31} = 0.34$, $P = 0.56$).

Dietary response.—More grasshoppers were fed to nestlings in 1990 than in 1991 ($t_{10} = 5.16$, $P < 0.001$; *t*-test), while greater numbers of Lepidoptera larvae and Diptera were fed to nestlings in 1991 than in 1990 ($t_{10} = 2.36$, $P = 0.02$; $t_{10} = 2.36$, $P = 0.02$; *t*-test; Table 2). There were no differences between years in the number of taxa fed to nestlings ($Z = 0.64$, $P = 0.52$; Wil-

TABLE 2. Food items (number with percent in parentheses) brought to the nestlings by adult Savannah Sparrows in years with high (1990) and low (1991) grasshopper abundance, on the Delta Agriculture Project, Alaska.

	1990	1991
Arachnida	36 (25.2)	34 (25.2)
Orthoptera	87 (60.8)	0 (0.0)
Neuroptera	0 (0.0)	1 (0.8)
Coleoptera		
Adult	0 (0.0)	8 (5.9)
Larvae	0 (0.0)	5 (3.7)
Lepidoptera		
Adult	2 (1.4)	3 (2.2)
Larvae	8 (5.6)	34 (25.2)
Diptera	3 (2.1)	16 (11.9)
Diptera*	7 (4.9)	6 (4.4)
Hymenoptera	0 (0.0)	28 (20.7)
Total	143 (100.0)	135 (100.0)

* Family Tipulidae.

coxon rank-sum). Although adults fed nestlings more often per hour in 1990 than in 1991 ($\bar{x} = 9.6 \pm 0.6, n = 11; \bar{x} = 7.3 \pm 0.7, n = 11; F_{1,20} = 6.57, P = 0.02$), when brood size of the observed nests was considered as a covariate there was no significant difference between years ($F_{2,19} = 2.12, P = 0.16$). Brood size of the observed nests differed between years (1990, $\bar{x} = 5.2 \pm 0.3, n = 11$; 1991, $\bar{x} = 4.2 \pm 0.3, n = 11; F_{1,20} = 6.37, P = 0.02$). If we consider brood sizes of only four or five nestlings, adults fed nestlings more per hour in 1990 than 1991 ($\bar{x} = 10.39 \pm 1.03, n = 5; \bar{x} = 7.97 \pm 0.66, n = 8; F_{1,11} = 4.39, P = 0.06$). Even though this difference is not statistically significant, the difference may shed light on

why nestlings grew larger in 1990 than in 1991. In addition, when brood size was controlled for, there was no difference in average length of foraging bouts between years (1990, $\bar{x} = 3.2 \pm 0.4$ min/bout, $n = 9$; 1991, $\bar{x} = 4.5 \pm 0.7$ min/bout, $n = 11; F_{2,17} = 0.49, P = 0.50$).

Reproductive response.—Predation rates on the study site were unusually low for a ground-nesting passerine (Miller and Knight 1993), with all nests (28 in 1990 and 37 in 1991) being successful. Clutch sizes ranged from two to six eggs per clutch in 1990 and four to five eggs per clutch in 1991 (1990, $\bar{x} = 5.00 \pm 0.22, n = 22$; 1991, $\bar{x} = 4.60 \pm 0.09, n = 32$). There was a significant difference in clutch size between years ($G_4 = 10.07, P = 0.04$). Hatching success was similar between 1990 and 1991 ($\bar{x} = 89.9 \pm 3.6\%; \bar{x} = 87.5 \pm 3.3\%; H_1 = 0.39, P = 0.53; KW$ test). The number of birds fledged per nest ranged from one to six birds per nest in 1990 and two to five birds per nest in 1991 (1990, $\bar{x} = 4.46 \pm 0.26, n = 28$; 1991, $\bar{x} = 3.85 \pm 0.16, n = 35; G_5 = 9.86, P = 0.08$). Fledging success was high in both 1990 and 1991 ($\bar{x} = 97.3 \pm 2.0\%; \bar{x} = 96.2 \pm 1.7\%; H_1 = 0.72, P = 0.40; KW$ test). The amount of time spent brooding the nestlings was similar between years ($F_{2,17} = 0.02, P = 0.90$).

Nestlings were larger in 1990 than 1991 (Table 3). When brood size was considered a covariate with year, mass on day 7 was significantly lower in 1991 than in 1990 ($\bar{x} = 13.23 \pm 0.24$ g, $n = 23$; $\bar{x} = 13.74 \pm 0.19$ g, $n = 22; F_{2,42} = 4.32, P = 0.04$). If evaluation of brood size is restricted to four- or five-nestling nests (thus eliminating the brood-size effect), mass on day

TABLE 3. Comparison of growth parameters ($\bar{x} \pm SE$) on days 4 ($n = 22$) and 7 ($n = 23$) for nestling Savannah Sparrows on the Delta Agriculture Project, Alaska for high (1990) and low (1991) grasshopper years.

Growth parameter	1990	1991	F*	P
Day 4				
Ninth-primary length (mm)	3.75 \pm 0.22	3.01 \pm 0.23	5.15	0.03
Tarsus length (mm)	14.35 \pm 0.28	13.89 \pm 0.25	1.28	0.27
Mass (g)	8.67 \pm 0.24	8.00 \pm 0.23	5.68	0.02
Day 7				
Ninth-primary length (mm)	14.43 \pm 0.41	14.04 \pm 0.24	0.17	0.69
Tarsus length (mm)	19.41 \pm 0.14	19.10 \pm 0.14	1.78	0.19
Mass (g)	13.74 \pm 0.19	13.23 \pm 0.24	4.32	0.04
Amount gained between days 4 and 7				
Primary growth (mm/day)	3.69 \pm 0.13	3.56 \pm 0.05	0.27	0.60
Tarsus growth (mm/day)	1.71 \pm 0.06	1.68 \pm 0.05	0.25	0.62
Mass gain (g/day)	1.72 \pm 0.37	1.68 \pm 0.35	0.38	0.54

* GLM with year and brood in model.

7 was still greater in 1990 than in 1991 ($\bar{x} = 13.79 \pm 0.18$ g, $n = 12$; $\bar{x} = 13.00 \pm 0.27$ g, $n = 18$; $F_{1,28} = 5.04$, $P = 0.03$). Growth parameters differed more on the first visit (day 4) between years, with 1990 measurements greater than 1991 (Table 3), suggesting the most vulnerable period for growth may be in the first few days after hatch, rather than from day 4 to day 7. This is reinforced by the similarity in the growth rates between years from day 4 to day 7 (Table 3). If this analysis is restricted to broods of four or five nestlings, measurements for mass and ninth primary on day 4 were still significantly lower in 1991 than 1990. Tarsus measurements for day 4 do not differ statistically between years ($F_{2,27} = 2.99$, $P = 0.10$).

Numerical response.—Densities of adult Savannah Sparrows increased by 42% between the high and low grasshopper years (1990, $\bar{x} = 1.9 \pm 0.3$ birds/ha; 1991, $\bar{x} = 2.7 \pm 0.5$ birds/ha). However, this increase was not statistically significant ($t_9 = 0.94$, $P = 0.19$).

DISCUSSION

Savannah Sparrows nesting on the Delta Agriculture Project showed a dietary and reproductive response to superabundant grasshopper populations, but demonstrated no statistically discernible numerical response. The dietary and reproductive responses witnessed in our study were in the predicted direction; however, the magnitude of the response did not reflect the overwhelming change in prey abundance between years.

Dietary response.—Dietary responses may reflect a change in diet or a change in feeding rates, and dietary responses to changes in food supply are common (Buckner and Turnock 1965, Zach and Falls 1975, Morse 1978, Strehl and White 1986, Steenhof and Kochert 1988, Crawford and Jennings 1989, Korpimäki and Norrdahl 1989, 1991). We observed a dietary response in that nestlings were not fed grasshoppers in the low grasshopper year. Lepidoptera larvae and Diptera were used in greater amounts during the low grasshopper year, presumably reflecting the decrease in grasshopper availability.

Fewer feeding trips were made by adults to nests during the low grasshopper year than during the high grasshopper year. Differences we observed in feeding rates probably reflected

brood-size differences rather than changes in food availability.

Reproductive response.—Numerous factors can affect clutch size in birds (Klomp 1970, Hussell 1972) including food availability (Martin 1987), and Lack (1966) postulated that clutch-size variation was correlated with food availability. Although some authors have indicated no increase in clutch size due to a natural increase in food resources (Sealy 1980, Davies and Lundberg 1985, Strehl and White 1986), others have documented a positive response of clutch size to food availability (MacArthur 1958, Zach and Falls 1975, Anderson 1977, Sealy 1978, Marr and Raitt 1983, Fleischer et al. 1985, Hussell and Quinney 1986). Savannah Sparrows in our study had larger clutch sizes when grasshoppers were abundant.

Egg laying was initiated when grasshoppers were hatching (mean initiation date in 1990 was 31 May) and at a time when many of the grasshoppers had already reached the second and third nymphal stages (1990 U.S. Dep. Agriculture internal report by Sluss and Franklin). Savannah Sparrows in our study may have responded to improved nutrition by laying more eggs (Klomp 1970, Slagsvold 1988). Marr and Raitt (1983) found that Cactus Wrens (*Campylorhynchus brunneicapillus*) responded to grasshopper emergence by increasing clutch size when grasshoppers were abundant. Grasshoppers are high in nutritional value, exceeding 50% in crude protein content (Ueckert et al. 1972, DeFoliart 1975). Protein is an important component in the diet of birds during egg laying (Robbins 1981).

Anderson (1977) reported higher fledging success in House Sparrows (*Passer domesticus*) in response to outbreaks of periodic cicadas (*Magicicada* spp.). Strehl and White (1986) also indicated greater fledging success and higher mean numbers of nestling Red-winged Blackbirds (*Agelaius phoeniceus*) fledged during a year with abundant food. Savannah Sparrows in our study fledged more nestlings per nest in the food-abundant year; however, the difference was not statistically significant. The difference was likely a reflection of the differences in clutch size because the percentage of nestlings surviving to fledging was nearly equal between years.

Nestling growth can be influenced by food availability (Anderson 1977, Bryant 1978, Strehl and White 1986); however, Wiens (1974, 1977) suggested food availability is not a factor lim-

iting nestling growth in shrub steppe and grassland habitat. Growth of nidicolous birds is illustrated by a sigmoid curve; growth occurs quickly during the first few days of life, then slows and may plateau by fledging (Ricklefs 1968, Maher 1973). Nutritious, abundant food may have a more important role in defining growth during the first one to four days of life for Savannah Sparrows. Growth slows between day 4 and 7, and the type and amount of food fed to the nestlings may not be as critical. Growth of nestling Savannah Sparrows in our study appeared to be more affected at day 4 than day 7. Ninth-primary measurements and mass were significantly lower in 1991 than 1990 on day 4. Tarsus measurements on day 4 were lower in 1991, however not significantly. In contrast, the only parameter that was significantly lower at day 7 in the year with few grasshoppers was mass, suggesting that retardation in growth occurred early in development. In addition, growth rates between day 4 and 7 did not differ between years. If, in fact, the vulnerable period of nestling growth occurs during the first four days of Savannah Sparrow development, our ability to detect strong differences in growth was low because of the developmental stage at which we took our measurements. The first four days may have dictated the growth patterns and final measurements of nestlings at day 7. This is supported by the significantly smaller measurements of ninth primary and mass at day 4 in 1991.

Numerical response.—A vertebrate population can experience a numerical response either by immigration or through recruitment (Solomon 1949). A numerical response depends on the mobility, reproductive potential and generation time of a predator (Korpimäki and Norrdahl 1991). Numerical responses by birds to natural fluctuations in prey density have been documented by numerous authors (Pitelka et al. 1955, Morris et al. 1958, Mebs 1964, Buckner and Turnock 1965, Southern 1970, Zach and Falls 1975, Morse 1978, Sealy 1980, Crawford and Jennings 1989, Korpimäki and Norrdahl 1989, 1991).

Crawford and Jennings (1989) suggested that Ruby-crowned Kinglets (*Regulus calendula*) showed a numerical response because their foraging ecology allowed them to encounter budworms in the early stages of infestation. However, in our study, emergence of grasshoppers probably occurred after territories were estab-

lished (yet prior to laying), so a within-season numerical response was probably unlikely.

Although our sampling method for arthropods other than grasshoppers was probably not adequate for a thorough inventory (Norment 1987), the method we used indicates fewer arthropods were available to Savannah Sparrows during the low grasshopper year. Savannah Sparrows were able to exploit successfully this substantially reduced food resource during the time when they were completing their breeding efforts during the low grasshopper year. This opportunistic behavior (Rotenberry 1980) suggests that Savannah Sparrows in our study were reproductively limited by factors other than food. Other authors have suggested that vegetative structure, territoriality, and carrying capacity are important in influencing reproductive output (Fretwell 1972, Wiens 1974, Ross 1980, Holmes et al. 1989, Holmes and Sherry 1992, Richner 1992).

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