

SURVIVAL AND GROWTH OF NESTLING VESPER SPARROWS EXPOSED TO EXPERIMENTAL FOOD REDUCTIONS¹

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Abstract. We examined the effects of experimental food reductions on the reproductive biology of nestling Vesper Sparrows (*Poocetes gramineus*) during 1991 in the Little Missouri National Grasslands, North Dakota. Grasshopper densities on territories around 24 individual nests were experimentally reduced while 31 nests served as controls. There were no significant differences between treatment and control nests in number of young fledged per nest, 2–8 day nestling growth rate, or final 8 day nestling mass. Nest failure was due to predation (83.3% of nests that failed), and abandonment or parental death (16.7% of nests that failed). Grasshoppers were the principal food, comprising 67.7% of all identified food items brought to all nests when nestlings were 7–8 days old. Breeding adults on treated territories foraged significantly further from the nest than control birds suggesting that birds on treated sites compensated for the reduction in food by altering foraging behavior.

Key words: *Food reduction; growth rates; Poocetes gramineus; reproduction; Vesper Sparrow; grasshoppers; carbaryl.*

INTRODUCTION

Various ecological patterns in avian systems are attributed to the availability of food, including clutch size, diet, habitat selection and territory placement, and reproductive success. Much of the evidence for food limitation of avian reproduction however, is correlative, and food availability is rarely quantified (Newton 1980). Experimental alteration of the food supply is the most direct way to address the question of food limitation (Newton 1980, Martin 1987). Experimentally supplemented food often yields increased clutch size, decreased nestling mortality, and increased nestling growth rates (Martin 1987, Boutin 1990). However increases in reproductive success when food is experimentally supplemented do not necessarily imply that natural food availability is low, but only that more food can be gathered for a given amount of time (Martin 1986). Of the few food reduction experiments to date, most have been conducted during periods of insect outbreaks and consequently have

not demonstrated a relationship between food abundance and bird reproduction (but see Rodenhouse and Holmes 1992).

In grassland ecosystems, two theories predominate on the role of food limitation during the breeding season. One assumes that food is limiting (Cody 1968). This view is supported by experimental studies that demonstrate that bird predation may reduce insect densities and species diversity, suggesting that some favored prey types may be limiting to birds (Joern 1986, Fowler et al. 1991, Bock et al. 1992, but see Belovsky et al. 1990), and an experiment that demonstrated optimal rather than opportunistic foraging in a population of grassland sparrows (Kaspari 1991). In contrast, Wiens and Rotenberry hypothesized that food for birds is often superabundant during the breeding season in grassland and shrubsteppe ecosystems (Wiens 1974; Wiens and Rotenberry 1979; Rotenberry 1980a, b). According to this view, periodically harsh years may reduce species richness and absolute numbers of birds, so that in the intervening years food resources are superabundant in relation to existing bird populations (Wiens 1974). Support comes from bioenergetic models that estimate that food consumption by birds is minor compared to total annual production (Wiens and Innis 1974, Wiens 1977) and from the high dietary overlap found among bird species, suggesting that

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bird species are not in competition for limited resources (Wiens and Rotenberry 1979). Direct examination of food limitation on individual reproductive success is needed in this system (Martin 1986).

Birds may respond to food-limitation by increasing energy expended in foraging. This may affect adult reproductive potential through: (1) decreased nest attentiveness; (2) delayed or reduced success of future broods; and (3) reduced parental survival (Martin 1987). Because foraging behavior is affected by food availability in some predictable ways and birds can rapidly adjust foraging behavior in response to prey availability, foraging behavior may indicate if birds perceive food to be limiting (Hutto 1990).

Here, we present results of a replicated field experiment in which grasshopper densities were reduced on territories of the Vesper Sparrow (*Poocetes gramineus*), a grassland passerine which preferentially forages for grasshoppers where available (Maher 1979). We addressed the null hypothesis that growth and survival of nestling Vesper Sparrows did not differ between territories where grasshopper densities were reduced and territories where food was not reduced. We also examined the following predictions of the food-limitation hypothesis: (1) nestling growth should vary inversely with brood size at treatment nests; and (2) nestling growth should vary positively with grasshopper density. In addition we examined the effect of a reduction in grasshopper densities on food delivery rate to the nest, foraging distance from the nest, and the proportional use of grasshoppers as nestling food.

METHODS

STUDY SITE AND NEST TREATMENT

Our study was conducted between 15 May and 17 August 1991, in the Little Missouri National Grasslands, McKenzie County, North Dakota. The open grassland habitat and topography are described in Fowler et al. (1991).

Vesper Sparrow nests were located by dragging a heavy rope (30 m long) over the ground and searching where adult birds flushed. Nests were marked with a stake and a small wooden stick placed 10 m and 1 m north of the nest, respectively. Nests with eggs were checked daily to determine hatch day. Nest searching began 15 May and continued until 5 August. Observations in previous years (1987–1990) indicated that this

is a conservative estimate of the breeding season (George and Adams, unpubl. data).

At hatching, each nest was designated as either treatment or control. Treatment assignments were made in a stratified manner to control for time of season, brood size, grasshopper density, vegetation, and weather. Only nests found during egg laying or incubation, and that had not been parasitized by Brown-headed Cowbirds (*Molothrus ater*), were used in this study.

When nestlings were 0–2 days old, we applied carbaryl bran bait to a large area (5.37 ± 3.42 ha/nest, range 3.11–11.97 ha) around each treated nest to reduce densities of grasshoppers, their preferred food item. Size of Vesper Sparrow territories ranges from 0.5–3.2 ha (Berger 1968, Wiens 1969, Rodenhouse and Best 1983). Our attempts to estimate territory size were not successful but observations of foraging adults indicated that individuals rarely flew outside the treatment boundaries.

Carbaryl bran bait is a federally registered grasshopper control agent (USDA 1987) which effectively reduces grasshopper densities (Onsager and Foster 1980, George et al. 1992). Studies have detected little or no direct toxicological effects of liquid carbaryl formulations on birds (Conner 1960, McEwen et al. 1972, McEwen 1981, Zinkl et al. 1977, DeWeese et al. 1979, Hill 1979, E.P.A. 1988). The bran bait formulation has even less potential for toxic effects on birds than liquid sprays because considerably less active ingredient is applied per ha and dermal, and inhalation exposure are eliminated (George et al. 1992). Carbaryl bran bait is produced commercially by mixing 40% carbaryl into flakes of wheat bran, at a rate yielding 1.96% active ingredient by weight in the field formulation. The bait is readily ingested by many species of grasshoppers, including the common species in our study area (Onsager and Foster 1980). Carbaryl bran bait was applied with a truck-mounted spreader at the rate of 2.24 kg/ha. The highest estimated potential cumulative dose of carbaryl our Vesper Sparrows could have received by ingesting poisoned grasshoppers was 12.9 mg/kg body mass, far less than the avian lethal dose of 707–2,000 mg/kg body mass (Smith 1987). Control nests received no carbaryl bran bait but the truck was driven over each area to simulate treatment.

We estimated grasshopper densities at each nest using 40 0.25 m² aluminum hoops arranged

in four rows of 10 hoops. Hoops were separated by about 5 m, both between and within rows. This method is a modification of that used by Onsager and Henry (1977). All rows of hoops were placed to one side of the nest, with the closest hoop about 10 m from the nest. Grasshoppers were counted before applying carbaryl bran bait and at two and six days post-treatment. We counted the number of grasshoppers within each hoop as they flushed at our approach. Vegetation within each hoop was brushed to flush any remaining grasshoppers.

WEATHER AND VEGETATION

For each nest we calculated the average daily maximum and minimum temperatures, and the total amount of rain that fell during the first eight days of the nestling period. We obtained daily maximum and minimum temperatures from a weather station that was centrally located in our study area. Rainfall data consisted of the mean from two weather stations, one 18.3 km north of the most northerly experimental nest, the other 23.3 km east of the most easterly nest.

A relative measure of the vertical density and height of grasses, forbs and shrubs was obtained at each nest using a Robel pole (height = 80 cm, diameter = 5 mm). The vegetation parameters were measured at 100 randomly selected points within a 100 by 100 m grid with the nest as its center. At each point, we recorded the number of stems or leaves touching each decimeter height interval of the pole. This method is a modification of that used by Wiens (1969) to describe grassland bird habitats. Vegetation variables that were highly correlated with each other, or for which there were few observations, were grouped together for analysis. This resulted in the following variables: number of grass or shrub hits between 0–19 cm, 20–39 cm, 40–79 cm; and number of forb hits between 0–19 cm, and 20–69 cm. We also measured vegetative cover over each nest (percent of a paper circle obscured by vegetation when placed on top of the nest cup and viewed from above), and the number of shrubs >30 cm in height within a 5 m radius of nest.

REPRODUCTIVE ECOLOGY OF VESPER SPARROWS

We marked nestlings for individual identification by painting the claws with nail polish. Nestlings were weighed to the nearest 0.25 g with a 30 g Pesola scale when two, four, and eight days

old. Some nestlings in asynchronous broods were weighed and measured at one, three, and seven days. We did not handle nestlings older than eight days because Vesper Sparrows fledge at about nine days (Rodenhouse and Best 1983).

A nest was judged successful, and included in the analysis, if ≥ 1 nestling survived to 8 days of age. To compare nestling growth between treated and control nests, we used 2–8 (or 1–7) day mass growth rates, as well as final eight (or seven) day mass. We calculated mass growth rates between days 2–8 for individual nestlings with the following equation (adjusted to include only daylight hours [05:00 to 22:00]):

$$\text{Growth rate} = \frac{M_8 - M_2}{\Delta t}$$

where:

M_8 = mass (g) on day 8,

M_2 = mass (g) on day 2, and

Δt = 6 days \times 17 hr daylight/days + (12 – hr weighed on day 1) + (hr weighed on day 8–12)

Because nestlings within a brood are not independent, we used a nest rather than a nestling as the experimental unit, and calculated growth rates and eight-day values for the mean of all nestlings within a brood. We also compared the growth variables for the youngest nestling (the smallest nestling at day 2) from each brood, as the youngest nestling may suffer higher mortality or slower growth during periods of food scarcity (Skagen 1987). Because food scarcity may result in brood reduction, we also examined growth data of nestlings that disappeared from otherwise successful nests for signs of starvation. Results are reported as the ratio of the 2–4 day growth rate of the nestling that disappeared, to the average 2–4 day growth rate of the remaining nestlings.

Because nestlings disappeared from some nests and brood size was not constant throughout the nestling period, we calculated an average brood size between the ages of two and eight days using the following equation:

$$\text{Brood size} = ((N_2 + N_4) + ((N_4 + N_8)2))/6,$$

where N_2 , N_4 , and N_8 are the number of nestlings present at two, four and eight days old, and six is the number of days between the visit on day 2 and on day 8.

We determined Vesper Sparrow foraging flight

distances, prey delivery rates, and items fed to 7–8 day old nestlings. We observed nests (control: $n = 16$ nests, $\bar{x} = 129.9 \pm 30.9$ min/nest, treated: $n = 13$, $\bar{x} = 132.0 \pm 21.3$ min/nest) from a blind (2 m high by 1.5 m diameter) placed about 10 m away. The blind was erected the day before observation to allow birds time to habituate. Foraging flight distance was visually estimated with the aid of small flags placed 25, 50 and 100 m from the nest. Food items were identified visually during the observation period as grasshoppers, Lepidoptera larvae, moths, beetles, or unknown. We could not identify prey items to species from 10 m away, and observation at closer distances disturbed the birds. Grasshopper and Lepidoptera use were calculated as the percentages of identified food items delivered to a nest.

ANALYSES

Repeated-measures ANOVA was used to analyze the grasshopper hoop count data because sequential counts are not independent (Beal and Khamis 1990). We transformed the hoop count data using $\ln(x + 1)$ to meet assumptions of normality.

We examined the relationship between treatment and growth variables using brood size, hatch date, and minimum average daily temperature during the nestling period as covariates, with treatment as the main effect, in an analysis of covariance. An examination of the effect of vegetation and weather variables on nestling growth indicated that minimum average daily temperature was significantly correlated with growth. Because hatch date had a bimodal distribution, for the ANCOVA we coded nests hatched prior to 18 June as 1, and nests hatched after 18 June as 2. We examined the following relationships with Spearman correlation coefficients: nestling growth and grasshopper density (using all nests), and nestling growth and brood size (using only treated nests). When a large number of correlation analyses was performed, we set the alpha level by dividing 0.05 by the number of correlations (Rice 1990).

We examined the relationship between treatment and foraging variables (food deliveries/hr, average foraging distance from nest, and grasshopper use) using hatch date, number of nestlings present during observation period, and treatment as the main effect in an analysis of covariance. Time of observation was non-signifi-

cant and dropped from this analysis. Nestling age was not used as a covariate because all observations occurred when nestlings were 7–8 days old. For all analyses of foraging data we used the average value per observation period for each variable.

RESULTS

We located 83 Vesper Sparrow nests. Twenty-eight nests (33.7%) failed before hatching. Losses were due to predation (23 nests) or abandonment (5 nests). Twenty-four of the remaining nests were treated with carbaryl bran bait and 31 served as controls.

The treatment effectively reduced grasshopper densities (Fig. 1). Whereas there was no difference in initial grasshopper densities between treated and control nests ($t = -0.161$, $df = 36$, $P = 0.87$), grasshopper densities decreased significantly over time relative to control nests (Greenhouse-Geisser adjusted F test for time* treatment effect, $F_{2,76} = 41.12$, $P < 0.001$).

Vegetation and weather did not differ among treated and control nests, nor did hatch date (Wilcoxon rank-sum test, $Z = 0.504$, $P = 0.615$, Fig. 2).

TREATMENT EFFECTS ON NESTLING SURVIVAL AND GROWTH

Of the control nests, 24 were successful (77.4%) and fledged 2.9 ± 1.18 nestlings/successful nest. Of the treated nests, 17 were successful (70.8%) and fledged 3.12 ± 1.36 nestlings/successful nest. Thirteen of the nest failures were due to predation and one treated nest was abandoned. There was no difference in the proportion of successful to unsuccessful nests between treated and control nests ($Z = 0.7913$, $P = 0.2144$). The number of nestlings hatched/nest did not differ between treated and control nests (two-tailed t -test, $P = 0.4256$) nor did the number of nestlings fledged/nest differ between treatments (two-tailed t -test, $P = 0.6168$). There was no indication that starvation caused the disappearance of nestlings from otherwise successful nests (treated nests: $n = 3$, 2–4 day growth rate of nestling that disappeared/average 2–4 day growth rate of remaining nestlings = 0.97 ± 0.05 , control nests: $n = 2$, 2–4 day growth rate of nestling that disappeared/average 2–4 day growth rate of remaining nestlings = 0.96 ± 0.11). There were no significant differences in the growth variables between treated and control nestlings (Table 1).

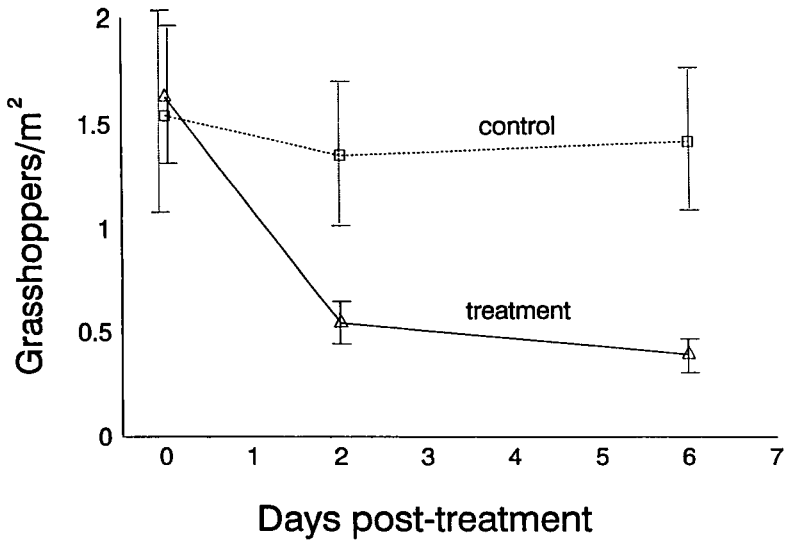


FIGURE 1. Change in grasshopper densities on areas around control and treated Vesper Sparrow nests over time. Means and \pm SE for each census sampling period (pre-treatment, two and six days post-treatment) are shown.

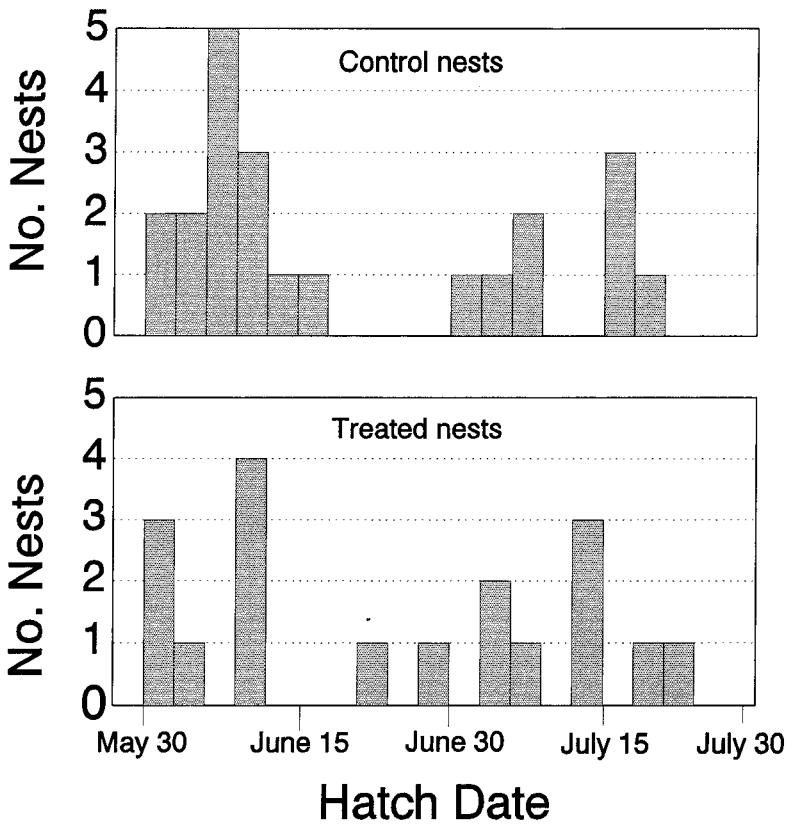


FIGURE 2. Seasonal distribution of control and treated Vesper Sparrow nests. Each bar represents the number of nests hatched within a three-day interval.

TABLE 1. Descriptive statistics for Vesper sparrow nestling growth variables at control and treated nests. *n* is the number of nests.

Growth variable	Control			Treated		
	<i>n</i>	\bar{x}	SD	<i>n</i>	\bar{x}	SD
Nest average						
Eight day mass (g)	22	17.61	1.36	16	17.91	2.53
Youngest nestling/nest						
Eight day mass (g)	18	16.37	1.90	13	17.54	2.54
Nest average						
2-8 day growth rate (g/d)	22	2.07	0.22	16	2.02	0.36
Youngest nestling/nest						
2-8 day growth rate (g/d)	17	2.07	0.31	13	2.09	0.33

Treatment did not contribute significantly to variation in nestling growth when hatch date, brood size, and minimum average daily temperature were used as covariates in an analysis of covariance (Table 2).

OTHER PREDICTIONS OF FOOD LIMITATION

Pre- or post-treatment grasshopper densities and nestling growth variables were not significantly

TABLE 2. Analysis of covariance of Vesper sparrow nestling growth variables with treatment as the main effect, and hatch date, brood size and minimum average daily temperature as covariates.

Source	df	<i>F</i>	<i>P</i>
Average eight day mass			
Treatment	1	0.00	0.964
Hatch date	1	0.20	0.656
Brood size	1	0.86	0.360
Temperature	1	8.29	0.007
Error	33		
Youngest nestling eight day mass			
Treatment	1	0.50	0.485
Hatch date	1	0.23	0.639
Brood size	1	0.12	0.733
Temperature	1	3.81	0.061
Error	26		
Average daily growth rate			
Treatment	1	0.69	0.412
Hatch date	1	0.46	0.504
Brood size	1	1.03	0.318
Temperature	1	3.24	0.081
Error	33		
Youngest nestling daily growth rate			
Treatment	1	0.09	0.762
Hatch date	1	1.75	0.198
Brood size	1	0.00	0.967
Temperature	1	0.25	0.620
Error	25		

correlated ($P > 0.024$ for all comparisons; alpha level 0.004, 12 comparisons). Brood size and nestling growth variables at treated nests were likewise not significantly correlated ($P > 0.354$ for all comparisons, alpha level 0.012, 4 comparisons).

FORAGING OBSERVATIONS

Adult Vesper Sparrows generally foraged on the treated areas. We were able to determine forage flight distance for 278 of 381 foraging trips. In flights of unknown distance, the bird usually disappeared from sight near the nest (24.5 ± 21.6 m from nest, range 15-100). Of known flight distances, only one flight of 200 m and two flights of 130 m were outside the treated areas (1.1%, all at treated nests).

Of the 296 identifiable food items delivered to nests (71% of all observations), 67.6% were grasshoppers, 29.0% were Lepidoptera larvae, and 3.4% were moths or beetles.

There were no significant differences between treated and control nests in the number of items delivered per foraging trip (Table 3). Treatment did not contribute significantly to variation in food deliveries/hr: variation in this parameter was explained largely by the number of nestlings present during the observation period (Table 4).

Treated and control nests did not differ in grasshopper use (Table 3) and grasshopper density was not correlated with grasshopper use (Spearman correlation coefficient, $P = 0.321$). Variation in grasshopper use was due largely to hatch date (Table 4). The correlation between Julian hatch date (rather than the 1 or 2 code used in the ANCOVA) and grasshopper use was significant: grasshopper use increased as the season progressed ($P = 0.0001$), while Lepidoptera larvae use decreased ($P = 0.0001$).

TABLE 3. Descriptive statistics and results of *t*-tests for foraging observation variables of control ($n = 16$) and treated ($n = 13$) Vesper sparrow nests. The mean values per nest were used to calculate values per treatment. For observation starting time, minutes were converted into fractions of hours.

	Control		Treated		<i>t</i> -test	
	\bar{x}	SD	\bar{x}	SD	<i>t</i>	<i>P</i>
Number foraging flights/hour	5.02	1.99	7.55	4.18	2.15	0.041
Food deliveries/hour	5.74	2.86	8.00	4.23	1.71	0.098
Flights of unknown distance/total flights	0.25	0.29	0.31	0.19	0.59	0.557
Average foraging flight distance	21.20	11.82	37.41	19.50	2.70	0.012
Maximum foraging flight distance	37.40	20.35	79.46	48.70	2.90	0.005
Number items delivered/foraging trip	1.10	0.25	1.10	0.27	0.03	0.977
Number grasshoppers/total number food items delivered to nest	0.59	0.28	0.62	0.28	0.31	0.761
Observation starting time	11.64	1.49	10.70	1.41	-1.70	0.100

Birds at treated nests foraged significantly further from the nest than birds at control nests (Table 3), and treatment contributed significantly to variation in foraging flight distance when the effects of hatch date and brood size are controlled for (Table 4).

We did not detect any significant relationships between the foraging variables examined and nestling growth variables (Spearman correlation coefficient, $P > 0.05$ for all comparisons, alpha level set at 0.004, 12 comparisons).

DISCUSSION

We did not detect any adverse effects on Vesper Sparrow nestlings due to reduction of grasshopper densities around nests. Although grasshoppers were a frequently consumed food source, there were no significant differences in nestling weights or growth rates between treated and control nests, and no evidence of starvation at treated nests.

Birds in food-reduced areas foraged significantly further from the nest than control birds. Central place foraging models, which assume optimal foraging, predict that birds feeding nestlings should forage closer to the nest on a territory where food supply is high, and forage further from the nest as food is depleted (Orians and Pearson 1979). Our results thus indicate that birds were foraging to maximize intake rates. This is counter to a prediction of the superabundant food hypothesis: that birds should not respond to different levels of food supply. Another prediction of central place foraging models, that birds should deliver more and larger prey with increasing distance from the nest, was supported by Kaspari's

work with Grasshopper Sparrows (*Ammodramus savaanarrum*) (Kaspari 1991).

Our study differed from other food limitation studies in species, environmental variables, and methodology. The one other study in which food was manipulated during the nestling period alone (Simons and Martin 1990) found that Cactus Wren (*Campylorhynchus brunneicapillus*) nestlings had higher survivorship, and greater mass and linear dimensions at food-supplemented nests. In contrast, we found no evidence of starvation or reduced nestling weight gains at food-reduced nests, although grasshopper density was reduced by about 70% during a year of naturally

TABLE 4. Analysis of covariance of foraging variables with treatment as the main effect, and hatch date and number of nestlings present during the observation period as covariates.

Source	df	<i>F</i>	<i>P</i>
Average foraging flight distance			
Treatment	1	8.10	0.009
Hatch date	1	5.77	0.024
Number nestlings	1	0.71	0.408
Error	25		
Food deliveries/hour			
Treatment	1	1.90	0.180
Hatch date	1	0.01	0.923
Number nestlings	1	7.07	0.014
Error	25		
Number grasshoppers/total number food items delivered to nest			
Treatment	1	1.74	0.199
Hatch date	1	4.07	0.054
Number nestlings	1	0.90	0.352
Error	25		

low grasshopper density (Keith Winks USDA, pers. comm.).

The natural brood sizes in our study may have been smaller than parents can provision, as has been found in other studies (Martin 1987). Although Vesper Sparrow brood size in our study area averaged about three nestlings, brood size ranged from 2–6 nestlings (178 nests, years 1989 and 1990, Adams, unpubl. data). Larger broods (4–6 nestlings) were not associated with increased starvation or decreased growth, indicating that three nestlings were fewer than the number that could be provided for. Small clutches may be selected for in fluctuating environments such as grasslands because larger clutches suffer lower reproductive success in food-poor years (Boyce and Perrins 1987). In addition to annual variation in food caused by environmental variables (e.g., previous years weather), grasslands are characterized by periodically harsh weather during the breeding season. Low temperatures significantly influenced nestling growth in our study. In addition to increasing thermoregulatory costs, cold weather may temporarily decrease food availability for birds as insects become less active and harder to detect. Increased time spent foraging decreases time available for brooding which may further increase thermoregulatory costs in nestlings. Consecutive days of cold weather may thus influence selection for smaller broods because large broods are difficult to provision during these periods. Food reduction would have less effect if selection results in clutch sizes adjusted to periods of low food availability.

Alternatively, factors other than food may select for small clutches. The most important cause of nest failure in our study was predation, a factor over which the parent birds may have little control. Because the risk of nest failure is high, the best reproductive strategy may be to maximize fitness through multiple small clutches rather than fewer large clutches.

Because parent birds can adjust foraging behavior to compensate for a reduction in food, reductions in nestling growth and survival may be evident only when food limitation is severe. Furthermore, other phases of reproduction, which we did not examine, may be more sensitive to food limitation. Renesting attempts often contribute significantly to annual productivity and can be affected by food limitation (Martin 1987, Simons and Martin 1990, Rodenhouse and

Holmes 1992). In our study, parent birds in food-reduced territories foraged further from the nest than control birds suggesting they were working harder to provision young. This could cause delayed or reduced success of future broods, or lower adult survival. Low food densities may also affect the post-fledging period. Sullivan (1989) found that while adult Juncos (*Junco phaeonotus*) maintained weight and provisioned four young while spending less than 75% of the daylight hours foraging, recently independent juveniles spent 90% of the daylight hours foraging. Thus, at very low food densities the lower proficiency of the fledglings at foraging may reduce survivorship.

Birds in our study delivered significantly more grasshoppers and fewer Lepidoptera larvae to nests as the season progressed. This was probably because grasshoppers grew in size and became more profitable prey, while Lepidoptera larvae metamorphosed and became less available. We found no evidence that nestling growth was affected by the seasonal change in diet (non-significant correlations between grasshopper use and growth variables, and non-significant contribution of hatch date in explaining variation in growth).

Other studies in grasslands that have directly examined the relationship between food availability and avian reproductive success have found no evidence of food limitation. Greer and Anderson (1989) found no relationship between arthropod productivity and nesting success, territory size, or population density of McCown's Longspurs (*Calcarius mccownii*), on a mixed-grass prairie in Wyoming. Bedard and Lapointe (1984) also found no relationship between food abundance and nesting success of Savannah Sparrows (*Passerculus sandwichensis*) nesting in abandoned fields. Our study similarly found no evidence that food was limiting based on measures of reproductive success. These results suggest that food in most years does not limit reproduction of grassland birds. Our foraging data suggest however that birds on food-reduced territories may compensate for the reduction in food by altering foraging behavior and effort.

ACKNOWLEDGMENTS

Our manuscript benefitted from readings by J. Wiens, W. Clements, A. Joern, and an anonymous reviewer. E. Cromie, S. Kittrel, R. Corcoran, J. Cook, E. Crow, M. Stratman, and D. Perriman assisted in fieldwork

and K. Burnham and O. Myers gave statistical advice. J. Jeske applied the carbaryl bran bait. Support for our study was provided by the U.S. Department of Agriculture APHIS Grasshopper Integrated Pest Management Project and Colorado State University.

LITERATURE CITED

- BEAL, K. G., AND K. J. KHAMIS. 1990. Statistical analysis of a problem data set: correlated observations. *Condor* 92:248-251.
- BEDARD, J., AND G. LAPOINTE. 1984. The Savannah Sparrow territorial system: can habitat features be related to breeding success? *Can. J. Zool.* 62:1819-1828.
- BELOVSKY, G. E., J. B. SLADE, AND B. A. STOCKHOFF. 1990. Susceptibility to predation for different grasshoppers: an experimental study. *Ecology* 71:624-634.
- BERGER, A. J. 1968. *Poocetus gramineus* Eastern Vesper Sparrow, p. 868-882. In O. L. Austin [ed.], Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies. U.S. Natl. Mus. Bull. 237, part 2.
- BOCK, C. E., J. H. BOCK, AND M. C. GRANT. 1992. Effects of bird predation on grasshopper densities in an Arizona grassland. *Ecology* 73:1706-1717.
- BOUTIN, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Can. J. Zool.* 68:203-220.
- BOYCE, M. S., AND C. M. PERRINS. 1987. Optimizing Great Tit clutch size in a fluctuating environment. *Ecology* 68:142-153.
- CODY, M. L. 1968. On the methods of resource division in grassland bird communities. *Am. Nat.* 102:107-147.
- CONNER, P. F. 1960. A study of small mammals, birds and other wildlife in an area sprayed with sevin. *N.Y. Fish Game J.* 7:26-32.
- DEWESE, L. R., C. J. HENNY, R. L. FLOYD, K. A. BOBAL, AND A. W. SCHULTZ. 1979. Response of breeding birds to aerial sprays of trichlorfon (dylor) and carbaryl (sevin-4-oil) in Montana forests. U.S. Dept. of Interior. Spec. Sci. Rept., Wildlife no. 224, Washington, DC.
- ENVIRONMENTAL PROTECTION AGENCY. 1988. Pesticide fact handbook. Noyes Data Corporation, Park Ridge, NJ.
- FOWLER, A. C., R. L. KNIGHT, T. L. GEORGE, AND L. C. McEWEN. 1991. Effects of avian predation on grasshopper populations in North Dakota grasslands. *Ecology* 72:1775-1781.
- GEORGE, T. L., L. C. McEWEN, AND A. FOWLER. 1992. Effects of a carbaryl bait treatment on nontarget wildlife. *Environ. Ent.* 21:1239-1247.
- GREER, R. D., AND S. H. ANDERSON. 1989. Relationships between population demography of McCown's Longspurs and habitat resources. *Condor* 91:609-619.
- HILL, E. F. 1979. Cholinesterase activity in Japanese Quail dusted with carbaryl. *Lab. Anim. Sci.* 29:349-352.
- HUTTO, R. L. 1990. Measuring the availability of food resources. *Studies in Avian Biology* 13:20-28.
- JOERN, A. 1986. Experimental study of avian predation on coexisting grasshopper populations (Orthoptera: Acrididae) in a sandhills grassland. *Oikos* 46:243-249.
- KASPARI, M. 1991. Central place foraging in Grasshopper Sparrows: opportunism or optimal foraging in a variable environment? *Oikos* 60:307-312.
- MAHER, W. J. 1979. Nestling diets of prairie passerines at Matador, Saskatchewan, Canada. *Ibis* 121:437-452.
- MARTIN, T. E. 1986. Competition in breeding birds: on the importance of considering processes at the level of the individual. *Curr. Ornithol.* 5:181-210.
- MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annu. Rev. Ecol. Syst.* 18:453-458.
- McEWEN, L. C. 1981. Review of grasshopper pesticides vs. rangeland wildlife and habitat, p. 362-382. In J. M. Peek and P. D. Dalke [eds.], Proceedings, wildlife-livestock relationships symposium. Univ. of Idaho, Moscow, ID.
- McEWEN, L. C., L. C. KNITTLE, AND M. L. RICHMOND. 1972. Wildlife effects from grasshopper insecticides sprayed on short-grass range. *J. Range Manage.* 25:188-194.
- NEWTON, I. 1980. The role of food in limiting bird numbers. *Ardea* 68:11-30.
- ONSAGER, J. A., AND J. E. HENRY. 1977. A method for estimating the density of rangeland grasshoppers (Orthoptera: Acrididae) in experimental plots. *Acrida* 6:231-237.
- ONSAGER, J. A., AND R. N. FOSTER. 1980. A model for predicting efficacy of carbaryl bait for control of rangeland grasshoppers. *J. Econ. Ent.* 73:726-729.
- ORIANI, G. H., AND N. E. PEARSON. 1979. On the theory of central place foraging, p. 154-177. In D. J. Horn, R. D. Mitchell, and G. R. Stairs [eds.], Analysis of ecological systems. Ohio State Univ. Press, Columbus, OH.
- RICE, W. R. 1990. A consensus combined P-value test and the family-wide significance of component tests. *Biometrics* 46:303-308.
- RODENHOUSE, N. L., AND L. B. BEST. 1983. Breeding ecology of Vesper Sparrows in corn and soybean fields. *Am. Midl. Nat.* 110:265-275.
- RODENHOUSE, N. L., AND R. T. HOLMES. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. *Ecology* 73:357-372.
- ROTENBERRY, J. T. 1980a. Bioenergetics and diet in a simple community of shrubsteppe birds. *Oecologia* (Berlin) 46:7-12.
- ROTENBERRY, J. T. 1980b. Dietary relationships among shrubsteppe birds: competition or opportunism in a variable environment? *Ecol. Monogr.* 50:93-110.
- SIMONS, L. S. AND T. E. MARTIN. 1990. Food limitation of avian reproduction: an experiment with the Cactus Wren. *Ecology* 71:869-876.
- SKAGEN, S. K. 1987. Hatching asynchrony in American Goldfinches: an experimental study. *Ecology* 68:1747-1759.
- SMITH, G. J. 1987. Pesticide use and toxicology in

- relation to wildlife: organophosphorus and carbamate compounds. U.S. Fish and Wildlife Service, Resource Publication 170, Washington, DC.
- SULLIVAN, K. A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phae-notus*). *J. Anim. Ecol.* 58:275-286.
- USDA. 1987. Final environmental impact statement, rangeland grasshopper cooperative management program. APHIS FEIS 87-1. U.S. Dept. of Agriculture, Hyattsville, MD.
- WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithol. Monogr.* 8, American Ornithologists' Union, Lawrence, KS.
- WIENS, J. A. 1974. Climatic instability and the "ecological saturation" of bird communities in North American grasslands. *Condor* 76:385-400.
- WIENS, J. A. 1977. Model estimation of energy flow in North American grassland bird communities. *Oecologia (Berlin)* 31:135-151.
- WIENS, J. A., AND G. S. INNIS. 1974. Estimation of energy flow in bird communities: a population bioenergetics model. *Ecology* 55:730-746.
- WIENS, J. A., AND J. T. ROTENBERRY. 1979. Diet niche relationships among North American grassland and shrubsteppe birds. *Oecologia* 42:453-492.
- ZINKL, J. G., C. C. HENNY, AND L. R. DEWEESE. 1977. Brain cholinesterase activities of birds from forests sprayed with trichlorfon (Dylox) and carbaryl (Sevin-4-oil). *Bull. Env. Cont. Toxicol.* 17:379-386.