

NESTLING BIOLOGY OF THE FIELD SPARROW

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ABSTRACT.—The biology of Field Sparrow nestlings was studied during two breeding seasons in central Illinois, on a 23.6-ha tract composed of mixed vegetation. Predominant nestling foods were lepidopteran larvae, orthopteran nymphs, homopterans, and spiders. Foods given to nestlings ranged in size from less than 0.005 cc to 0.38 cc, the upper size limit increasing with nestling age. The food size class most frequently fed to the young contained items smaller than 0.05 cc, although its importance decreased as the nestlings grew older. Girth rather than length limited the size of food the young successfully ingested. The number of feeding trips per hour to 6-day-old broods ranged from 0 to 21 and averaged 9, divided about equally between male and female. The feeding frequency peaked shortly after dawn and just before dusk, and was lowest near midday. There was a significant inverse relationship between the female feeding rate and brooding time. Ambient temperature significantly influenced brooding time, with the least brooding at 60° to 69°F. The rate of feeding individual nestlings decreased slightly (nonsignificant) as brood size increased. The overall nestling growth rate index (weight) averaged 0.568, and ranged 0.444 to 0.712. No nestling starvation was evident. The rate of weight gain in broods of four was significantly higher during early summer than late summer, while broods of three showed a significant opposite trend. The dependence of thermoregulatory maintenance costs upon brood size is discussed. Growth rates of the youngest nestlings were significantly less than those of their siblings. It was concluded that Field Sparrows forage opportunistically for their nestlings, and that food availability did not limit breeding success on the study tract.—*Department of Ecology, Ethology, and Evolution, University of Illinois, Champaign, Illinois 61820. Present address: Department of Animal Ecology, Iowa State University, Ames, Iowa 50010. Accepted 30 October 1975.*

THE nestling period is one of the most critical intervals in the lives of birds. Energetic demands on the parent birds to procure food are maximal, susceptibility of the nest to predation is frequently at its greatest, and limited food resources often result in differential nestling growth ultimately affecting pre- and postfledging survival. Despite the importance of the nestling period, good quantitative field data on many facets of this stage in the avian life cycle are lacking. The literature is replete with tabulations of nestling weight gain, but factors influencing growth rate, foraging patterns of adult birds when procuring nestling food, and patterns of feeding the young in the nest, are frequently overlooked. Nestling food habits data are also generally fragmentary and sample sizes small. Such was the state of knowledge for the Field Sparrow (*Spizella pusilla*).

METHODS

I studied the breeding ecology of a Field Sparrow population during the spring and summer of 1971 and 1972 at Allerton Park, 7 km southwest of Monticello, Piatt County, Illinois. The periphery of the 23.6-ha study area was shrub-woodland, with central regions of shrub-grassland and grassland (Best 1974).

Nestling weight and tarsal length were recorded daily between 1100 and 1300. Immediately after weighing, nestling food items were sampled by attaching ligatures around the throats to prevent swallowing. The ligatures were left on the young for approximately 1 hour after they were returned to the nest. Nestlings 6 days and older were not disturbed to avoid the risk of inducing premature departure from the nest (Walkinshaw 1939). Food volume was determined by water displacement.

Parents feeding nestlings 6 days after hatching were watched from a blind at 11 nest sites. At most, one nestling of the brood was 5 days old, the others were 6 days old. This age was selected as food could not be sampled, and young 6 days old will not normally fledge unless disturbed (Walkinshaw 1939). At each nest the observation periods covered the following time intervals: dawn–0800, 0900–1200, 1300–1600, and 1700–dusk. A mirror positioned above the nest permitted observation of its contents. Adults and nestlings were marked with colored leg bands.

Significance for statistical analyses was set at $P \leq 0.05$.

TABLE 1
MAJOR FOODS GIVEN TO FIELD SPARROW NESTLINGS DURING THE SUMMERS OF 1971 AND 1972

Taxa	% of total numbers		% of total volume	
	1971	1972	1971	1972
Lepidoptera (larvae)	37	30	56	47
Orthoptera (nymphs)	15	18 ¹	14	22
Homoptera	16	22	2	16
Spiders	14	22	6	12
Other	18	8	22	3
TOTAL	92	163	7.86 ²	14.12

¹ Includes 2 adult orthopterans.

² Volume in cc.

RESULTS AND DISCUSSION

NESTLING FOOD HABITS

Foods presented to nestlings.—Adult Field Sparrows fed their young a variety of animal material (for a complete listing see Best 1974). Predominant foods included lepidopteran larvae, orthopteran nymphs, various homopterans, and spiders (Table 1) (see also Evans 1964). Lepidopteran larvae decreased in the diet from 1971 to 1972, while orthopteran nymphs, homopterans, and spiders increased. The most noticeable increase was in the volume of homopterans, resulting from 13-year cicadas (*Magicicada* sp.) emerging.

Seasonal distribution of nestling foods.—The relative importance of the major nestling foods changed considerably during both breeding seasons (Fig. 1). Volumetric rather than numerical data are presented, because they reflect more accurately the food resource potential of each major food group. Homopterans were negligible in the nestling diet prior to July in 1971, but comprised a substantial portion of the early summer food in 1972. This resulted from the emergence of 13-year cicadas, which constituted an extremely abundant alternate food source from the end of May throughout June. Lepidopteran larvae were by far the most important food in May and June diets, reached their lowest level in July, and increased again in August. This pattern was consistent for both years. Lepidopteran larvae have been reported to decrease in the diet of nestling Song Sparrows (*Melospiza melodia*) and House Sparrows (*Passer domesticus*) toward the end of the breeding season (Tompa 1962, Seel 1969). During both years, orthopterans were absent from the May nestling diet, of minor importance during June, but contributed the largest percentage to the total food volume in July and August. Robins (1971) noted few orthopterans present in the nestling Henslow's Sparrow (*Ammodramus henslowii*) diet prior to mid-July. In 1971 spiders were an important food source in May (only three food items were collected that month), but decreased to negligible levels after June. During the summer of 1972 spiders comprised a rather constant proportion of the total food volume.

Although inconsistencies between years in the proportion of various foods in the nestling diet may result from sampling error, availability of food resources is probably of greater import (e.g. homopterans). Seasonal shifts in foods given to Field Sparrow nestlings probably resulted largely from the interaction between variation in availability of each individual food source and the abundance of alternate food items. There were also indications that the adults' foraging patterns changed as the season advanced.

Distribution of foods according to nestling age.—Spiders consistently decreased in

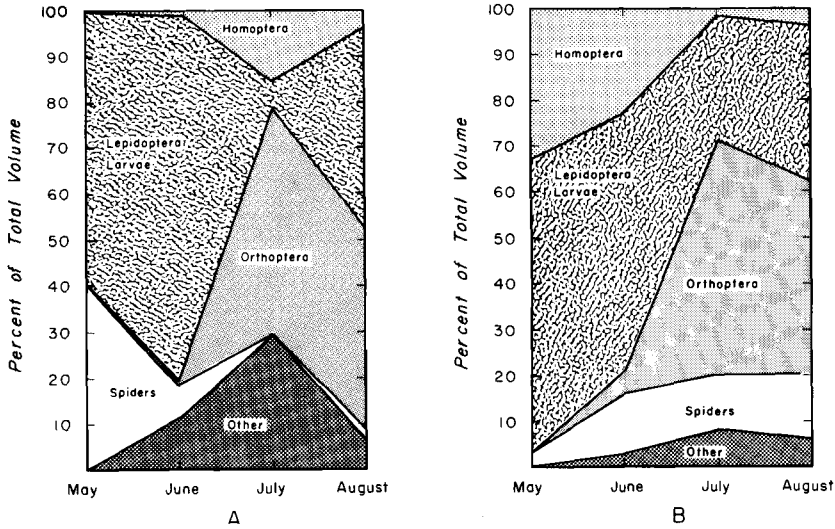


Fig. 1. Seasonal distribution of major foods given to Field Sparrow nestlings during 1971 (A) and 1972 (B).

the diet as nestlings grew older, while orthopterans increased (Fig. 2). The larger size of orthopterans probably restricted their occurrence in the diet of younger nestlings (see below). Homopterans comprised a nearly constant proportion of the nestling diet, while lepidopteran larvae fluctuated erratically with increasing age. Aside from size, differences in the nutritional quality of various foods could influence dietary changes as the nestlings grow older. Spiders (Fautin 1941, Betts 1955, Royama 1970) and lepidopteran larvae (Gross 1921, Betts 1955) decrease in the nestling diet of other passerines as the young grow older, while orthopterans (Gross 1921, Fautin 1941, Robins 1971) increase. Royama suggested that spiders have special nutritional value, important for nestling growth at an early stage.

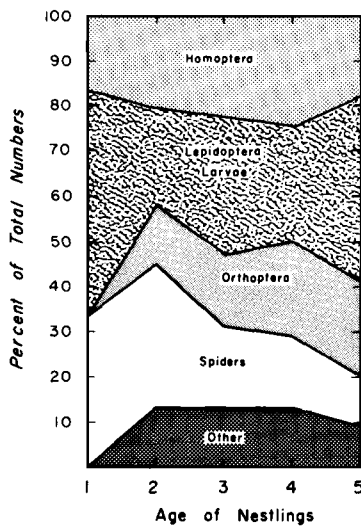


Fig. 2. Distribution of major foods among nestlings of different age (age = days after hatching).

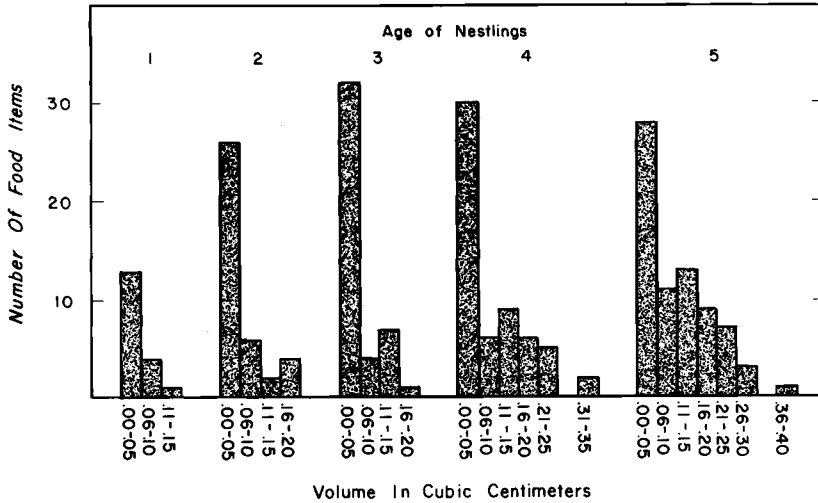


Fig. 3. Size of food items given to nestlings from 1 to 5 days old.

Food size.—The size of foods given to the nestlings ranged widely from less than 0.005 cc to 0.38 cc, the upper size limit increasing with nestling age (Fig. 3). Food items smaller than 0.05 cc occurred more frequently in the diet than any other size class, although their relative importance decreased as the nestlings grew older and were fed a wider size range of foods. Persistence in feeding small food items to older nestlings, capable of ingesting much larger material, was unexpected as the energy content per unit item would be much less in smaller foods. Feeding smaller foods may persist from foraging habits and/or “specific searching images” (Tinbergen 1960) developed early in the nestling period, may result from opportunistic foraging where foods smaller than 0.05 cc are more plentiful and/or easier to capture, or be due to certain nutritional needs satisfied only by smaller food items. Most of the very small food items were homopterans.

The tendency to feed older nestlings larger items was observed within all four major food groups (Best 1974). Either earlier developmental stages were given to smaller nestlings, or different taxa were selected as the nestling period progressed. Some food species were given to nestlings of all ages, either because of their small size or by selecting earlier instars for younger nestlings.

Girth rather than length of prey limited the size of foods successfully fed to 6-day-old nestlings. Thirteen-year cicadas had the largest diameter of all foods. Although only the abdomen, and occasionally the thorax, were fed to the nestlings, these often required compaction and softening by the parent's bill before successful ingestion. Other large-girth food items were prepared similarly. In contrast, walkingsticks (family Phasmidae) 8 cm long were easily swallowed once one end was introduced into the nestling's mouth.

Food alteration prior to feeding nestlings.—Individual food items were often fragmented when given to nestlings. Although the bodies of lepidopteran larvae were always intact, the head capsules were frequently disrupted or even removed. Bateman and Balda (1973) made a similar observation and concluded that the larvae were captured by grasping the head. Wings were absent on large moths, but generally present on small ones. Most grasshoppers were entire, although sometimes the hind

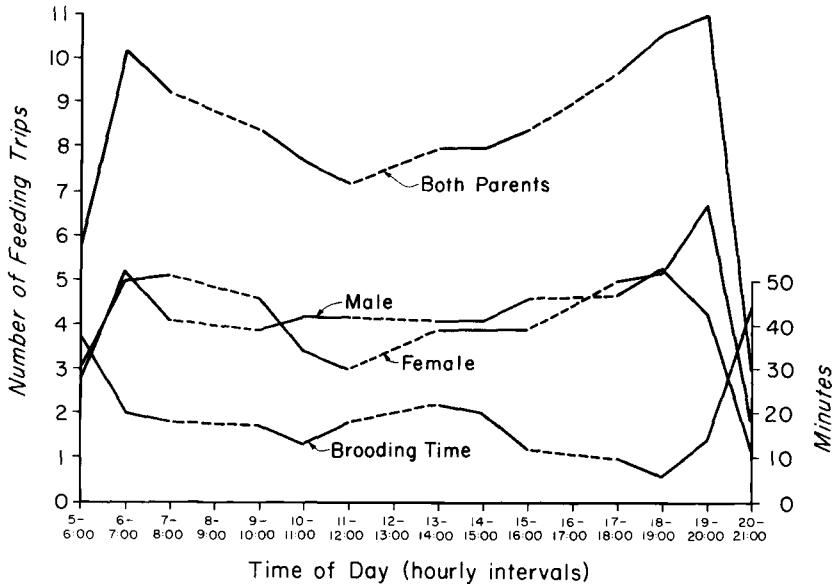


Fig. 4. Distribution of feeding trips and brooding time for 6-day-old nestlings throughout the day. The plotted values represent mean number of feeding trips and mean brooding time sampled from nine broods and eight broods, respectively. Time = Daylight Savings Time.

legs and occasionally the other legs and head were missing. Legs were generally removed from walkingsticks. Spiders had a variable number of legs missing; occasionally only the abdomen was present. Almost all small homopterans were intact. The wings, legs, head, and usually the thorax were removed from 13-year cicadas. Much food fragmentation probably occurred during capture, although some undoubtedly served to reduce food size for swallowing, particularly in the 13-year cicadas. Fragmentation or partial mastication of large food items by parent birds to facilitate ingestion by nestlings has also been observed in other species (Stewart 1953, Tinbergen 1960).

FEEDING AND FORAGING PATTERNS

General information.—The number of feeding trips per hour ranged from 0 to 21 and averaged 9 for broods containing 6-day-old young. The time interval between successive trips varied from a few seconds (when both parents arrived at the nest simultaneously and fed the young in turn) to 84 minutes (much of the time while the female brooded two nestlings during light rain). The mean was 7 minutes. The average time interval between feedings reported elsewhere for nestlings of comparable age ranges from 6 to 10 minutes (Jones 1913, Walkinshaw 1939, Crooks 1948). The male and female divided the task of feeding the young about equally (Fig. 4, see also Crooks and Hendrickson 1953). Adults carried from one to several food items on each foray, depending largely on size; smaller items were carried in greater numbers. Generally the food collected during each feeding trip was given to a single nestling, sometimes to two, and rarely to three.

The present discussion uses feeding frequency and feeding rate synonymously, although variability in the size and number of food items brought per visit may result

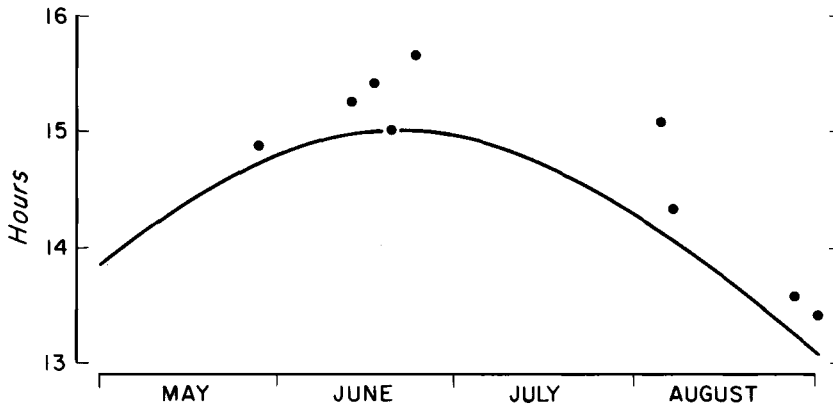


Fig. 5. Relationship between the potential foraging period (see text) and photoperiod. The line represents the time interval between sunrise and sunset. The dots indicate the foraging periods observed during the breeding season.

in feeding frequencies that do not reflect the true feeding rate (i.e. the quantity of food per unit time fed to the nestlings) (Gibb and Betts 1963, Royama 1966).

Distribution of feeding trips throughout the day.—The intensity of feeding 6-day-old nestlings peaked twice throughout the day, once shortly after dawn and again before dusk, just following and prior to spending the night brooding the young (Fig. 4). Both sexes showed this feeding pattern, although the females contributed disproportionately more to the feeding effort during the early morning and early evening. The lowest feeding rate occurred near midday. Females were largely responsible for this reduction, probably because of the increased time spent brooding near midday. The feeding frequency by males remained relatively constant from midmorning until late afternoon. Crooks (1948) and Walkinshaw (1968) also reported lower feeding rates near midday than in the evening. High feeding intensity in the morning and late afternoon or early evening with minimal feeding near midday has been reported in other species (Fautin 1941, Kluver 1950, Dunnet 1955, Kessel 1957).

Relationship between potential foraging period and photoperiod.—The potential foraging period for nestling food (the interval between the female's first departure from the nest in the morning until she remained to brood that evening) increased as days lengthened (Fig. 5). The foraging period in June was approximately 2 hours longer than in late August. The influence of photoperiod on the daily food intake and growth rate (weight) of nestlings was determined using a partial correlational analysis with brood size held statistically constant. There was a nonsignificant, inverse relationship between the number of feeding trips per nestling per day and

TABLE 2
MEAN NUMBER OF FEEDING TRIPS PER NESTLING PER DAY¹ IN RELATION TO BROOD SIZE

	Brood size		
	2 (2) ²	3 (3)	4 (4)
Male	13.8	17.1	16.6
Female	23.3	18.3	14.5
Total trips	37.1	35.4	31.1

¹ Three hours of feeding time are excluded from each daily interval.

² Number of broods sampled.

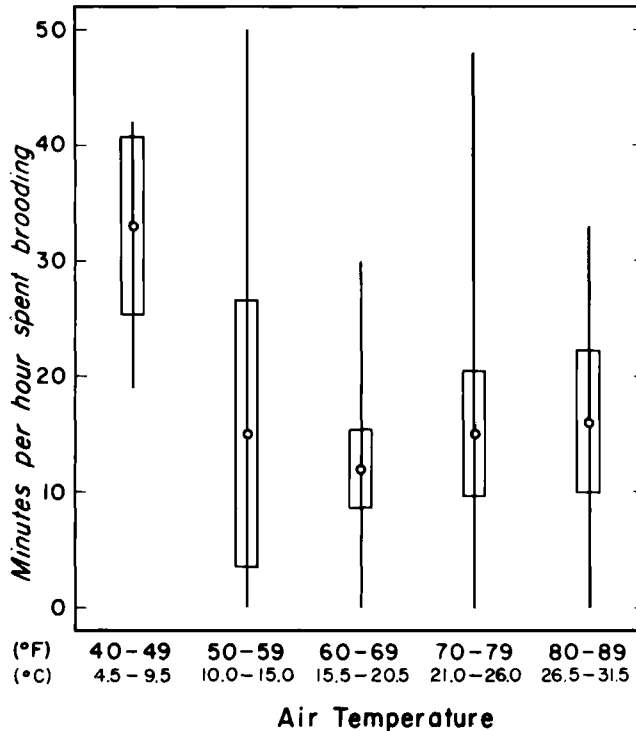


Fig. 6. Relationship between brooding time and ambient temperature. The mean, two standard errors and range are presented for each temperature class. (The hour intervals during which the female first left the nest in the morning and when she stayed on the nest to brood for the night were excluded.)

length of photoperiod ($r = -0.547$, $n = 9$), suggesting that increased day length did not enhance the daily food intake of nestlings, but the quantity of food carried per foraging trip was not measured and may have changed during the season (see Gibb and Betts 1963, Royama 1966). The relationship between day length and growth rate was also nonsignificant.

Factors influencing the frequency of feeding trips.—A correlational analysis was made between the number of feeding trips by females and the time spent brooding, taken at hourly intervals. Data were collected on 10 different days and from 7 different females. All time spent at the nest, excluding feeding, was considered brooding, whether the female's body extended partially or wholly over the nestlings. There was a highly significant, inverse relationship between feeding rate and brooding time ($r = -0.505$, $n = 115$). This implies that factors increasing brooding time also reduce the feeding frequency by decreasing the time available for the female to

TABLE 3
SEASONAL DISTRIBUTION OF MANDIBLE TYPES IN LEPIDOPTERAN LARVAE FED TO FIELD SPARROW NESTLINGS¹

Mandible type	May	June	July	August
Grasses	1	13	1	6
Herbaceous vegetation	1	12	2	8
Trees and shrubs	8	10	2	4

¹ Includes only larvae for which the mandible type could be determined (82% of the total sample). Values = number of larvae.

TABLE 4
SEASONAL DISTRIBUTION OF GROUND AND LOW VEGETATION SPIDERS FED TO FIELD SPARROW NESTLINGS¹

Location	May	June	July	August
Ground	0	1	2	3
Low vegetation	2	21	6	13

¹ Values = number of spiders.

forage. Inverse relationships between brooding times and feeding rates have been reported also in the House Wren (*Troglodytes aedon*) (Kendeigh 1952) and House Sparrow (Seel 1960).

The relationship between hourly brooding time and ambient temperature (taken at 10°F intervals) was tested using a one-way analysis of variance. The differences in brooding time among the temperature classes proved highly significant ($F = 3.56$, $df = 4, 95$), mainly the result of the notably longer brooding time when the temperature ranged between 40° and 49° (Fig. 6). The mean brooding time was lowest at 60° to 69° and increased with either lower or higher temperatures. The large variation in brooding time within each temperature class suggests considerable variability in the response of females to temperature. Differences in brood size and temperature at the immediate nest vicinity may have influenced this. The dependency of brooding time on ambient temperature would be greater earlier in the nestling period, as the ability to thermoregulate increases with nestling age (Dawson and Evans 1957) with a concomitant decrease in diurnal brooding (Walkinshaw 1939, Crooks and Hendrickson 1953).

Although the total number of feeding trips by both parents increased with brood size, the rate of feeding individual 6-day-old nestlings decreased slightly (Table 2). Also the proportion of the total feeding trips made by the male increased as the brood became larger. Neither of the latter two trends was statistically significant (two-way analysis of variance). Seel (1969) reported that the shares of the sexes in feeding nestling House Sparrows was independent of brood size.

Foraging sites.—Patterns in foraging for nestling food shifted as the breeding season advanced. Lepidopteran larvae were classified by the type of vegetation upon which they fed, using mandible morphology (Table 3). Most larvae given to May nestlings came from trees and shrubs, but by August foraging in woody vegetation appeared somewhat limited. A seasonal transition also occurred among spiders found in the nestling diet (Table 4). Ground spiders were absent in May foods, but occupied an increasing proportion of the arachnid diet as the season progressed. Limited field

TABLE 5
WEIGHT AND TARSAL LENGTH OF NESTLING FIELD SPARROWS

Age (days after hatching)	Sample size	Weight (g)			Tarsal length (cm)		
		Mean	SD	Range	Mean	SD	Range
0	47	1.48	0.16	1.23-1.90	.71	0.03	.60-.75
1	56	2.28	0.33	1.78-3.18	.87	0.06	.75-1.00
2	58	3.52	0.50	2.67-5.06	1.09	0.07	1.00-1.20
3	57	5.05	0.66	3.69-7.07	1.34	0.09	1.15-1.55
4	52	6.53	0.69	5.44-8.35	1.56	0.10	1.30-1.80
5	38	7.87	0.75	6.63-9.55	1.76	0.08	1.55-1.95

TABLE 6
NESTLING GROWTH RATE IN RELATION TO BROOD SIZE AND TIME OF SEASON

Brood size ²	Sample size ³	Early summer ¹				Late summer ¹				
		Weight		Tarsal length		Sample size	Weight		Tarsal length	
		Mean	SD	Mean	SD		Mean	SD	Mean	SD
3	9	.524	.030	.461	.046	12	.572	.048	.440	.038
4	24	.589	.056	.506	.086	3	.513	.041	.452	.033

¹ Early summer = before 15 July, late summer = after 15 July.

² Broods of 2 young were not included because of small sample size.

³ Sample size = number of nestlings.

observations also revealed that adults tended to forage for nestling food in wooded areas early in the breeding season but utilized more open sites with low-level vegetation toward the end of the season (see also Royama 1970). Individual pairs were seen foraging in different locations for later broods.

NESTLING GROWTH

Growth pattern.—Table 5 shows the weight gain and increment in tarsal length of nestling Field Sparrows from 0 to 5 days after hatching. Variability in both weight and tarsal length increased with age. Tarsal length was less variable than weight for nestlings of all ages, indicating that bone growth is less influenced by extrinsic factors, and suggesting greater reliability in using tarsal length to determine the age of nestlings whose hatching date is unknown.

Mean nestling weight on my study tract for ages 0 through 5 days was consistently less than that reported by Walkinshaw (1939) and Dawson and Evans (1957), the differences being statistically significant for all ages when compared with Dawson and Evans' data (*t*-test of means). (Walkinshaw's data could not be compared statistically.) Lower mean weight even on the day of hatching suggests possible inherent differences in growth rate prior to hatching.

Overall growth rate.—The overall growth rate index (*K*) of each nestling was determined using a graphical method of fitting equations to growth curves (Ricklefs 1967). The growth curve of the Field Sparrow is best approximated by the logistic growth equation, with a weight asymptote of 11.0 g (Ricklefs 1968) and a tarsal length asymptote of 2.10 cm.

The overall growth rate index (weight gain) of 58 nestlings from 18 broods averaged 0.568, and ranged from 0.444 to 0.712. Ricklefs (1968) calculated the growth rate of nestling Field Sparrows to be 0.656 from data presented by Walkinshaw (1936) and 0.640 from information reported by Dawson and Evans (1957), both studies conducted in Michigan. The lower nestling growth rate on my study area may have resulted from differences in nestling food between Illinois and Michigan. My sampling the food presented to each brood for 1 hour during midday probably impeded growth very little, because the feeding rate was lowest at this time, thereby minimizing the proportion of the total daily food intake removed. Geographic differences in growth rate have also been noted in other species (reviewed in Ricklefs 1968).

The relationship between growth rate of the tarsus and that of body weight was not statistically significant ($r = 0.141$, $n = 58$). Apparently factors influencing bone

growth operate independently of those responsible for weight increases. Ricklefs (1968) noted that, "The development of more stable anatomical . . . features may proceed independently of weight."

Factors influencing growth rate.—The influence of brood size and the time of season on growth rate was analyzed by a *t*-test of means. Comparisons between the early and late summer periods (before and after 15 July) within broods of a given size and between broods of different size within the same period showed no significant differences in tarsal growth rate. The rate of nestling weight gain in broods of four was significantly higher during early summer than late summer ($t = 2.24$, $df = 25$) (Table 6). A significant, but opposite trend was found in broods of three ($t = 2.62$, $df = 19$). Weight gain during early summer was significantly higher in broods with four nestlings than in those with three ($t = 3.27$, $df = 31$). The differences during late summer were not significant.

Availability of nestling food probably did not influence the growth rate significantly. The accelerated growth in 4- versus 3-nestling broods in early summer, and the increase in the growth rate of 3-nestling broods as the season advanced with a concomitant decrease in 4-nestling broods, cannot be explained on the basis of a limiting food supply. Heat conservation and dissipation are dependent upon the exposed surface to volume ratio, which brood size may alter significantly. Royama (1966) reported an inverse relationship between food consumption per nestling and brood size in the Great Tit (*Parus major*), and suggested that the lower surface to volume ratio in larger broods lessened the heat loss per nestling. Mertens (1969) confirmed that when nestlings were maintained at the mean ambient temperature, heat production per nestling varied inversely with brood size.

A lower surface to volume ratio may be advantageous when ambient temperatures are below an optimum, through minimizing heat loss, but when the temperature exceeds optimum, reduced surface area becomes disadvantageous by limiting the dissipation of excess heat. Westerterp (1973: Fig. 7) presented data showing an increase in the metabolic rate of Starling (*Sturnus vulgaris*) broods above and below a certain temperature optimum. The proportion of consumed energy devoted to growth is inversely related to the energetic costs of thermoregulation. Four-nestling broods may have lower maintenance costs early in the summer than 3-nestling broods, with the converse being true during late summer, but when the mean nestling growth rate of each brood was plotted against the mean temperature during the nestling period, the growth rate of different-sized broods showed no differential response to ambient temperature. According to Van Balen (1973), air temperature did not significantly influence the growth rate of nestling Great Tits. In neither study were the temperatures measured at nest sites; temperature variation in the immediate nest vicinity may have differed from the values used in the analyses. More study is needed to verify the interaction effects of brood size and ambient temperature on nestling growth.

Differences in growth rate between the youngest nestling (hatched 1 day later than the others) and the average for the remaining nestlings of each brood were analyzed using a paired *t*-test. Growth rates in weight and tarsal length were both significantly lower in the youngest nestlings ($t = 3.33$, $df = 9$; $t = 2.96$, $df = 9$), indicating a competitive disadvantage in late hatching. As no mortality from starvation occurred during the 2 years of my study, the reduced growth rate probably was not critical to nestling survival, but differential mortality resulting from variable nestling weight may not become evident until after the young fledge (see Lack 1966, Perrins 1965).

CONCLUDING COMMENTS

The Field Sparrow is apparently opportunistic when foraging for its nestlings. It feeds its young a diversity of animal taxa ranging widely in size and alters foraging patterns in response to fluctuations in the food supply. Seasonal changes in nestling diet and foraging patterns undoubtedly reflect variation in food availability. This could result in a temporal shift in territory quality as measured by its food resource potential for nestlings.

All evidence suggests that availability of nestling food did not limit breeding success on the study area. The feeding frequency did not appear restricted by the adults' capacity to procure food, as the feeding rate varied widely, even within a single hour, and the number of feeding trips per nestling was not significantly greater in smaller broods. Although the growth rates of the youngest brood members were significantly less than those of their siblings, this does not necessarily imply limited food resources, but rather the intensity of internestling competition. Asynchronous hatching, occurring in most Field Sparrow broods, has been considered an adaptation to a highly variable food supply (Lack 1954, 1966, 1968; Ricklefs 1965). In the present study no nestlings died from starvation, again suggesting that food was abundant. Evans (1964) also concluded that nestling food was not in limited supply in an old field in Michigan.

The absence of a significant difference in feeding rate per nestling among broods of different size, but the presence of significant differences in growth rates, indicates that factors other than the availability of nestling food may affect nestling growth. The dependence of thermoregulatory maintenance costs upon the surface to volume ratio of broods may be such a factor.

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