

GROWTH OF NESTLING SAGE SPARROWS AND BREWER'S SPARROWS

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ABSTRACT.—From 1980-1984, we characterized Sage Sparrow (*Amphispiza belli*) and Brewer's Sparrow (*Spizella breweri*) nestling growth and evaluated proximate factors potentially influencing growth in a southeastern Idaho shrubsteppe community. Increase in mass and tarsus length of both species was best explained by a logistic equation. For Sage Sparrows, all growth parameters we estimated varied significantly among years; 1983 seemed especially favorable for growth. Sage Sparrow mass growth rate and tarsus length at age 8 days declined significantly later in the breeding season, and tarsus growth rate varied inversely with brood size. In general, daily maximum temperature was negatively correlated with Sage Sparrow growth; weather seemed to have more effect early in the nestling period than later. Infestations of flesh fly larvae (Sarcophagidae) on Sage Sparrow nestlings were associated with reduced tarsus length near fledging. Little variation in Brewer's Sparrow nestling growth was explained by the variables we measured. Mass growth rate varied significantly among years and throughout the breeding season. Mass attained by age 7 days was greater in larger broods, but this effect was confounded by interactions among brood size, year, and seasonal effects. Received 6 Dec. 1985, accepted 7 Apr. 1986.

The diversity in growth patterns among birds is well documented (Ricklefs 1968). The pattern and rate of growth of a particular species ultimately may be determined by such factors as food availability (Lack 1968), predation pressure (Ricklefs 1984), or physiological considerations (Ricklefs 1979). Variation in rate and magnitude of growth within a species may be considerable (Zach and Mayoh 1982), and, although some of it likely reflects genetic variability within the species (e.g., Smith and Dhondt 1980), much of it may be attributed to the effects of extrinsic factors. For example, brood size (Best 1977, Bryant 1978), year (Ricklefs and Peters 1979, Price 1985), season (Best 1977, Ross 1980), habitat (Ross 1980, Rogers 1985), weather (Bryant 1975, Murphy 1985), and ectoparasites (Winterstein and Raitt 1983, Arendt 1985a) can influence nestling growth.

The Sage Sparrow (*Amphispiza belli*) and Brewer's Sparrow (*Spizella breweri*) are common species breeding in the Great Basin of the western United States (Wiens and Rotenberry 1981). Although considerable recent research effort has focused on the breeding ecology of these species (e.g., Wiens and Rotenberry 1979, 1981; Petersen and Best 1985), there is no published information on nestling growth. Documenting growth is desir-

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able because it is potentially influenced by a variety of factors and thus may yield insight into other facets of the breeding ecology of these species. For example, growth rates might be used as indicators of territory quality or of stress resulting from environmental perturbation (Fendley and Brisbin 1977).

Our objectives were to (1) describe growth of nestling Sage and Brewer's sparrows and (2) evaluate the effects of year, season, brood size, weather, and ectoparasites on growth rate and magnitude. Few investigators have studied growth of a species for more than 3 breeding seasons. Our 5-year study contributes to our understanding of long-term variation in growth and provides a reliable data base from which to evaluate factors affecting nestling growth.

STUDY AREA AND METHODS

Our study area was on the Idaho National Engineering Laboratory (INEL) site, 11 km south of Howe, Butte County, Idaho. The INEL site comprises sagebrush (*Artemisia* spp.) shrubsteppe habitat at an elevation of about 1500 m on the upper Snake River plain. Average annual precipitation is about 20 cm (Anderson and Holte 1981). Major shrub species were big sagebrush (*A. tridentata*) and green rabbitbrush (*Chrysothamnus viscidiflorus*); dominant grasses included bluebunch wheatgrass (*Agropyron spicatum*) and Indian rice grass (*Oryzopsis hymenoides*). Forbs were sparse, and much of the ground was bare.

Data were collected in the breeding seasons of 1980–1984. We initially established four 6.25-ha plots 200 m apart from each other, and additional data were collected in 1982–1983 from a 12-ha plot 1 km away. The latter plot had vegetation composition nearly identical to that on the 6.25-ha plots. Two of the 6.25-ha plots were partly burned in September 1981, and the 12-ha plot was partly burned in September 1982. In 1982, Sage Sparrow mass growth data from two of the 6.25-ha plots differed slightly but significantly from those of the other three plots, but in other years growth did not vary among plots. Thus, we pooled data across plots.

All plots were searched systematically for nests using a rope-drag technique (Petersen and Best 1985) that flushed attending adults from their nests. Many nests also were discovered incidental to our other field activities. Active nests were visited at 1- or 2-day intervals. During visits after hatching, each nestling's mass was measured to 0.1 g with a Pesola scale; left tarsus length was measured to 0.01 cm with calipers. Nestlings discovered within 4–5 days after hatching were aged by reference to the sample of known-age nestlings and were included in mean growth curves (Fig. 1). However, they were not used to calculate growth rates of individual broods and were excluded from all statistical tests.

Daily weather information, measured at Howe, was obtained from the National Climatic Center, Asheville, North Carolina. For each brood, we calculated mean daily maximum temperature and total precipitation for the entire period over which we measured the nestlings of that brood, and also for the first and second halves of the nestling period (0–4 and >4 days of age for Sage Sparrows, 0–3 and >3 days for Brewer's Sparrows). Each year, we calculated mean daily maximum temperature and total precipitation for the brood-rearing portion of the breeding season (approximately June–July) and also for the 2-month period (approximately April–May) preceding the appearance of most nestlings.

Most investigators who have modeled passerine growth have done so by using a logistic model. Accordingly, we described Sage and Brewer's sparrow growth with the logistic equa-

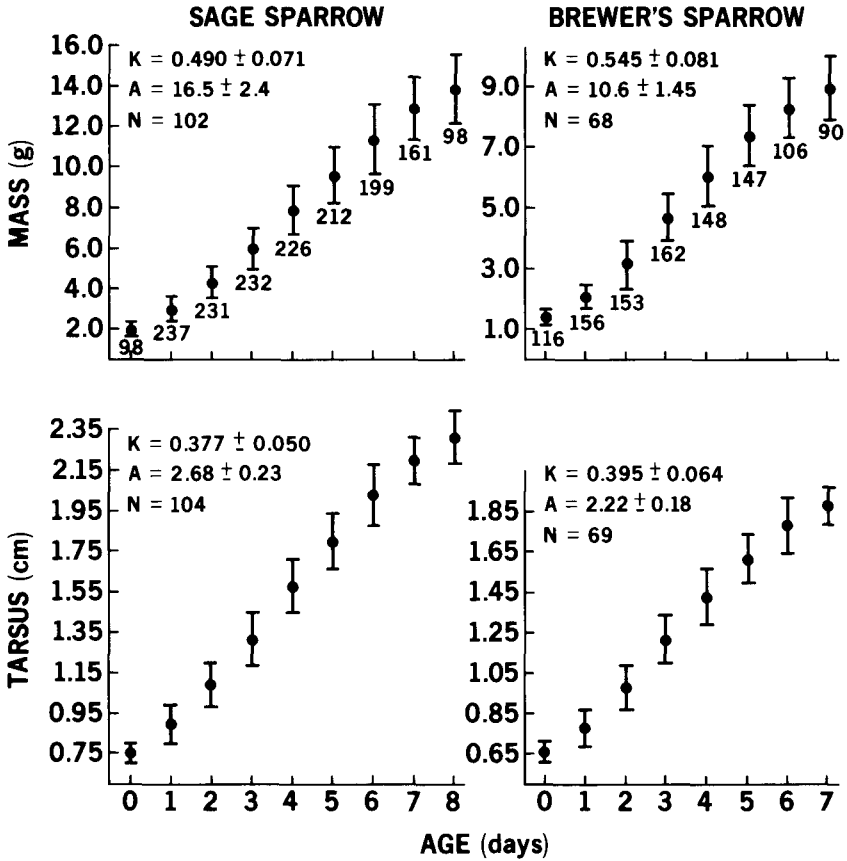


FIG. 1. Sage and Brewer's sparrow growth curves for mass and tarsus length. Dots and vertical bars represent $\bar{x} \pm SD$; values below the bars are numbers of nestlings measured. K = growth rate constant (days^{-1}), A = asymptote (g or cm), and N = number of broods sampled.

tion, $Y(t) = A / \{1 + \exp[-K(t - I)]\}$, where $Y(t)$ is the mass or tarsus length at age t days, A is the asymptote of the growth curve, K is a constant (days^{-1}) describing the rate at which the asymptote is achieved, and I is the age at the inflection point of the growth curve. Curve asymptotes were estimated, and curves were fitted to data by Ricklefs' (1967) graphical procedure. As Ricklefs recommended, we often adjusted asymptotes several times to obtain best-fit curves. As a further justification for our selecting the logistic model rather than a linear model to evaluate growth, we calculated coefficients of determination (r^2) for the mean growth curves (Fig. 1), using both models. Coefficients for the logistic model ranged from 0.997 to 0.999; those for the linear model were always less. We evaluated magnitude of growth by using measurements taken at age 7 (Brewer's Sparrow) or 8 (Sage Sparrow) days. (Brewer's Sparrows normally fledged at 8–9 days, Sage Sparrows at 9–10 days.)

For all statistical tests, broods, rather than individual nestlings, were used as sample units because measurements of nestlings within a brood were not independent. Three-way analysis of variance was used to examine variation in growth rate and in magnitude of growth among years, semimonthly periods of the breeding season (1–15 June, 16–30 June, etc.; each brood was assigned to a period based on hatching date), and brood sizes. Broods incurring partial loss of nestlings during the nestling period were not considered in analysis of brood size. *t*-tests were used to compare growth between broods with ($> \frac{1}{2}$ of the nestlings parasitized) and without (0 nestlings parasitized) infestations of flesh fly larvae. In none of our analyses were variances significantly heterogeneous. We used partial correlation analysis, with the effects of brood size statistically held constant, to evaluate relationships between growth parameters and weather variables. Unless stated otherwise, statistical significance was set at $P \leq 0.05$.

RESULTS AND DISCUSSION

General growth information.—Changes in mass and tarsus length (Fig. 1) followed the sigmoid pattern common to many other passerines (Ricklefs 1968). On the day of hatching (age 0), measurements were relatively constant among nestlings of each species, but variation increased steadily as nestlings aged. Growth curves only began to level off about 1 day before fledging. Thus, growth was incomplete at fledging (see also, Austin and Ricklefs 1977, Rogers 1985). This could be an adaptation to decrease the time exposed to predators while in the nest, thereby enhancing survival (Ricklefs 1969).

Mean growth rate constants for mass (Fig. 1) were similar to those of other similar-sized emberizids (e.g., Ricklefs 1968, Maher 1973, Best 1977). Tarsus length increased at a substantially slower rate than mass; the mean tarsus growth rate constant for Brewer's Sparrows was considerably less than that reported by Best (1977) for the Field Sparrow (*S. pusilla*), a congener of the Brewer's Sparrow.

Ricklefs (1968) noted that R-values (ratio of asymptote to adult size) for mass were usually less than 1 for ground- and foliage-foraging species but often greater than 1 for aerial foragers. Because of the necessity for flight, aerial foragers must be well developed at fledging. Neither Sage Sparrows nor Brewer's Sparrows forage aerially (Winter 1984), and their R-values for mass were 0.85 and 0.97, respectively. (Adult sizes were obtained from mist-netted birds [Petersen 1982]; SS: mass = 19.3 ± 1.2 g [SD], tarsus length = 2.54 ± 0.08 cm, N = 166; BS: mass = 10.9 ± 0.7 g, tarsus length = 2.04 ± 0.05 cm, N = 83.) In general, Brewer's Sparrows fly more often during forays than do Sage Sparrows (Winter 1984), and this may account for the difference in R-values. Interestingly, R-values for tarsus length were greater than 1 for both species (SS: 1.06, BS: 1.09), suggesting the importance of early development of pedal locomotion.

Annual variation.—Growth rate and magnitude varied significantly among years for Sage Sparrows (Table 1). From 1980 to 1981, mass growth

TABLE 1
RESULTS OF 3-WAY ANALYSES OF VARIANCE OF NESTLING SAGE AND BREWER'S SPARROW GROWTH RATE CONSTANTS (K), AND MASS AND TARSUS LENGTH (TL) NEAR FLEDGING (AGES 8 AND 7 DAYS FOR THE TWO SPECIES, RESPECTIVELY) IN RELATION TO YEAR, PERIOD IN THE BREEDING SEASON, AND BROOD SIZE

Source	Sage Sparrow						Brewer's Sparrow					
	Growth rate (K)			Measurements at age 8 days			Growth rate (K)			Measurements at age 7 days		
	df	Mass	TL	df	Mass	TL	df	Mass	TL	df	Mass	TL
Year	4	2.50 ^a	5.01 ^a	4	5.76 ^a	8.10 ^a	4	2.73 ^a	1.30	4	1.68	1.25
Semimonthly period ^b	3	2.91 ^a	2.27	3	2.79	3.82 ^a	2	5.39 ^a	1.46	2	1.36	1.15
Brood size	3	0.24	4.42 ^a	3	0.39	1.38	2	1.63	1.76	2	15.45 ^a	0.04
Year × period	9	0.42	0.47	8	1.92	1.06	7	0.99	0.68	6	9.67 ^a	1.32
Year × brood size	12	0.61	0.88	8	0.84	0.88	7	1.05	0.66	3	9.36 ^a	0.22
Period × brood size	8	0.88	1.02	3	0.44	1.22	4	1.42	0.11	3	19.03 ^a	0.86
Year × period × brood size	5	0.91	2.17	0	—	—	4	0.42	0.49	1	31.87 ^a	1.27
Residual	54			20			35			17		

^a F-values are significant ($P \leq 0.05$).

^b 1-15 June, 16-30 June, etc.; each brood was assigned to one period, based on hatching date.

TABLE 2
SAGE AND BREWER'S SPARROW NESTLING GROWTH PARAMETERS (MEAN ± SD) THAT VARIED SIGNIFICANTLY AMONG YEARS

Year	Sage Sparrow				Brewer's Sparrow			
	Growth rate (K)		Measurements at age 8 days		Growth rate (K)		Mass	
	N ^a	Mass	Tarsus length	N ^a	Mass (g)	Tarsus length (cm)	N ^a	Mass
1980	17	0.484 ± 0.066	0.354 ± 0.045	12	14.4 ± 1.4	2.36 ± 0.08	16	0.577 ± 0.084
1981	20	0.459 ± 0.047	0.358 ± 0.027	9	13.6 ± 1.7	2.30 ± 0.09	13	0.509 ± 0.053
1982	22	0.497 ± 0.098	0.392 ± 0.060	16	12.6 ± 2.1	2.22 ± 0.15	11	0.579 ± 0.066
1983	29	0.517 ± 0.076	0.397 ± 0.054	18	14.7 ± 1.1	2.36 ± 0.13	14	0.520 ± 0.097
1984	16	0.480 ± 0.054	0.369 ± 0.038	4	15.3 ± 2.0	2.35 ± 0.03	15	0.540 ± 0.079

^a Number of broods sampled.

rate decreased while tarsus growth rate was nearly constant; measurements at age 8 days declined from 1980 to 1981 (Table 2). From 1981 to 1982, growth rates increased while mass and tarsus length at age 8 days again declined. All parameters increased in 1983, but in 1984 growth rates declined, mass at age 8 increased, and tarsus length was constant. Clearly, 1983 was the most favorable year for Sage Sparrow growth; all parameters were at or near their greatest values. In 1982, growth rates were quite high, but mass and tarsus length at age 8 days were at their lowest levels.

For Brewer's Sparrows, only mass growth rate varied significantly among years (Table 1). Moreover, annual variation in Brewer's Sparrow mass growth rate did not parallel that of Sage Sparrows (Table 2); means were greatest in 1980 and 1982, and least in 1981. Evidently, either different factors caused annual growth variation in the two species, or they were influenced by the same factors in different ways.

Weather and food potentially cause annual variation in growth. Weather can influence growth directly through its effects on physiology or indirectly through its effects on food supply. Price (1985) documented annual variation in growth of Darwin's finches (*Geospiza fortis*) and attributed it to weather-mediated fluctuations in the food supply. Sage Sparrow annual mean tarsus growth rate varied inversely with mean daily maximum temperature during April and May ($r = -0.97$, $df = 3$) but not with mean daily maximum temperature during the brood-rearing portion of the breeding season (June–July, $r = -0.02$). Although we did not measure annual fluctuation in available foods, we did sample nestling diets in 1980–1983 (Petersen and Best 1986). Sage Sparrow annual mean mass growth rate varied with the percentage contribution of Lepidoptera larvae (the major food) to the diet ($r = 0.94$, $df = 2$, $P = 0.06$). Thus, some of the annual variation in Sage Sparrow growth may have resulted from effects of early-season temperatures on nestling foods. Annual variation in total precipitation was not significantly correlated with annual variation in Sage Sparrow growth. Brewer's Sparrow growth was not correlated with annual variation in any weather parameter.

Seasonal variation.—Sage Sparrow mass growth rate and tarsus length at age 8 days varied significantly among semimonthly periods of the breeding season (Table 1). Mass growth rate was high throughout June, but less for broods hatching in July; tarsus length at age 8 days declined slightly, but steadily, throughout the breeding season (Table 3). Brewer's Sparrow mass growth rate also varied among periods of the breeding season (Table 1). From early to late June, the mean growth rate constant increased; in early July, it was sharply reduced (Table 3). (Nearly all Brewer's Sparrow nesting was completed before late July.) Other investigators also have documented seasonal declines in growth parameters (e.g., Bryant 1978, Ricklefs and Peters 1979).

TABLE 3
SAGE AND BREWER'S SPARROW NESTLING GROWTH PARAMETERS (MEAN \pm SD) THAT
VARIED SIGNIFICANTLY AMONG SEMIMONTHLY PERIODS OF THE BREEDING SEASON

Period	Sage Sparrow				Brewer's Sparrow	
	Mass growth rate (K)	N ^a	Tarsus length at age 8 days (cm)	N ^a	Mass growth rate (K)	N ^a
1-15 June ^b	0.502 \pm 0.052	23	2.38 \pm 0.07	12	0.536 \pm 0.092	19
16-30 June	0.505 \pm 0.060	26	2.34 \pm 0.09	16	0.579 \pm 0.070	28
1-15 July	0.492 \pm 0.088	38	2.31 \pm 0.11	22	0.505 \pm 0.068	19
16-31 July	0.446 \pm 0.052	13	2.25 \pm 0.07	6		

^a Number of broods sampled.

^b Each brood was assigned to one period, based on hatching date.

Several factors likely account for seasonal changes in growth. Daily maximum temperatures increased throughout the breeding season (early June: \bar{x} = 20°C, late July: \bar{x} = 30°C), and sparrow growth may have been inhibited by high temperatures in July (see also, Murphy 1985). Alternatively, seasonal fluctuations in potential nestling foods may have influenced growth. For example, seasonal variation in mass growth rate in both species roughly paralleled the abundance of sagebrush arthropods sampled by Winter (1984) in 1983. Both species forage heavily in sagebrush. Van Balen (1973) found a positive relationship between caterpillar density and asymptotic mass of Great Tits (*Parus major*). Similarly, Bryant (1975) documented a significant relationship between House Martin (*Delichon urbica*) growth and insect abundance. A third possible explanation for seasonal declines in growth is that adults become more taxed energetically as the season progresses (Morton et al. 1973, Biermann and Sealy 1985) and are unable to sustain high feeding rates.

Effects of brood size.—In general, brood size did not strongly influence Sage and Brewer's sparrow growth (Table 1); only two parameters varied significantly. For Sage Sparrows, tarsus growth rate was less in larger broods (b1: K = 0.406 \pm 0.070, N = 7 broods; b2: 0.386 \pm 0.051, N = 28; b3: 0.377 \pm 0.050, N = 43; b4: 0.368 \pm 0.036, N = 23); suggesting some limitation in the abilities of adults to provide food to larger broods. But tarsus length at age 8 days was not significantly related to brood size. Several investigators have documented negative effects of brood size on growth parameters (e.g., van Balen 1973, Bryant 1978). For Brewer's Sparrows, mass at age 7 days was significantly greater in larger broods (b2: \bar{x} = 8.1 \pm 3.2 g, N = 7; b3: 9.0 \pm 0.7 g, N = 20; b4: 9.2 \pm 0.8 g, N = 13); but because brood size interacted significantly with year and semi-

TABLE 4
SIGNIFICANT ($P \leq 0.01$) PARTIAL CORRELATIONS BETWEEN WEATHER VARIABLES AND SAGE SPARROW GROWTH RATE CONSTANTS (K) AND MEASUREMENTS AT AGE 8 DAYS (BROOD SIZE WAS CONTROLLED STATISTICALLY IN THE ANALYSIS)

Weather variable*	K (df = 87)		Measurements at age 8 days (df = 36)	
	Mass	Tarsus length	Mass	Tarsus length
TEMP	-0.29	-0.33		-0.47
TEMP1	-0.30	-0.30		-0.41
TEMP2			-0.48	-0.47
PRECIP				0.52
PRECIP1				0.48

* TEMP: mean daily maximum temperature over the entire nestling period; TEMP1: mean temperature over the first half (age 0–4 days) of the nestling period; TEMP2: mean temperature over the second half (>4 days) of the nestling period; PRECIP: total precipitation over the entire nestling period; PRECIP1: precipitation over the first half of the nestling period.

monthly period (Table 1), the effect of brood size was not consistent for all seasonal periods and all years (see also Best 1977).

Effects of weather. — When growth parameters for individual Sage Sparrow broods and their corresponding weather data were analyzed, a number of significant correlations emerged (Table 4). By contrast, Brewer's Sparrow growth was not correlated with weather, suggesting that either Brewer's Sparrows were more independent of environmental conditions or that conditions were more constant during their growth period. Brewer's Sparrows began nesting 1–2 weeks later and ended nesting about 2 weeks earlier than Sage Sparrows, but their nestlings did not encounter a narrower range of weather conditions.

Sage Sparrow growth rate constants and measurements at age 8 days were, in general, negatively correlated with temperature (Table 4). Precipitation was positively correlated with tarsus length at age 8 days, but precipitation was greatest early in the season when temperatures were cool. O'Connor (1977) and Murphy (1985) documented negative relationships between temperature and nestling size in the species they studied. Murphy suggested that heat stress resulting in mass loss was the primary reason for the relationship, but he also speculated that high temperatures may have impaired the ability of adults to forage and that assimilation efficiency may have decreased in extreme heat.

Weather seemed to influence growth more strongly early than late in the nestling period of individual broods. Four correlations (Table 4) involve weather effects in the first half of the nestling period (0–4 days of age), two in the second half (>4 days). This is not surprising as young

nestlings have poor thermoregulatory capabilities (e.g., Austin and Ricklefs 1977), whereas older nestlings, having developed endothermy, are better buffered from fluctuations in ambient temperature.

Effects of ectoparasites.—About 14% of all Sage Sparrow broods and 4% of all Brewer's Sparrow broods were parasitized by flesh fly larvae. For Brewer's Sparrows, fly parasitism did not significantly affect growth rate constants or mean mass or tarsus length at age 7 days. For Sage Sparrows, growth rate constants were not influenced by parasitism; however, parasitized broods had reduced tarsus lengths near the end of the nestling period. Mean values at ages 6 (1.93 ± 0.15 cm, $N = 11$ broods) and 7 days (2.12 ± 0.11 cm, $N = 13$) were significantly less than those for unparasitized broods (age 6 days: 2.04 ± 0.10 cm, $N = 82$, $t = 3.2$; age 7 days: 2.22 ± 0.10 cm, $N = 72$, $t = 3.3$); the mean value at age 8 days (parasitized: 2.24 ± 0.14 cm, $N = 8$; unparasitized: 2.32 ± 0.13 cm, $N = 51$; $t = 1.7$, $P = 0.10$) was nearly so. If reduction of nestling mass occurred, we could not detect it; larval biomass may have compensated for any mass lost by nestlings (see also Winterstein and Raitt 1983, Arendt 1985a). Young nestlings exhibited no reduction in size, but larval infestations usually were not evident until near the midpoint of the nestling period.

Nestling mortality attributable to fly parasitism was rare. Larvae usually evacuated just before nestlings fledged, and perhaps nestlings subsequently compensated for any previous reduction in growth. Gold and Dahlsten (1983), however, noted that stress at specific times may impede growth without the possibility of compensation even if the stress is later relieved. If growth reduction was not recovered, postfledging survival could have been reduced (see also Gold and Dahlsten 1983, Arendt 1985b).

Conclusions.—Growth in nestling Sage and Brewer's sparrows conforms to the general pattern documented for most passerines. Growth parameters were variable, and much of the variation in Sage Sparrow growth could be accounted for by differences among years, periods of the breeding season, and brood sizes, and by the effects of weather and ectoparasites. Overall, Brewer's Sparrow growth varied nearly as much as that for Sage Sparrows but was poorly explained by the variables that we measured. Food supply, an important component of the environment that we did not quantify, may have influenced growth in Brewer's Sparrows.

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