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GROWTH RATE AND DETERMINANTS OF FLEDGLING WEIGHT IN MICHIGAN-BREEDING SAVANNAH SPARROWS

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Fledgling body mass has long been considered an indicator of survivorship probability in avian populations (Perrins 1965, Newton et al. 1983). Individual variation in mass presumably reflects variation in critical fat reserves that, in turn, leads to differential survivorship among fledglings. I here report an analysis of variation in an estimate of fledgling mass of Savannah Sparrows (*Passerculus sandwichensis*) in relation to environmental (e.g., habitat type, territory size) and brood-related (e.g., brood size) factors. My purpose was to investigate the influences of proximate environmental factors upon potential survivorship. Because survivorship is an important aspect of natural populations, elucidation of such factors should lend insight into environmental influence upon population structure and dynamics.

MATERIALS AND METHODS

I gathered data on nestling body mass and growth rate in connection with a study of determinants of breeding territory size of sparrows inhabiting a portion of the south campus of Michigan State University in East Lansing, Michigan. The study area was an annually mowed, short-grass field surrounding two ca. 8-ha and three smaller ponds. Broods supplying weight data were verified as first broods of the 1982 breeding season; observations in 1981 showed the study population to be double-brooded, with predation on eggs or young closely followed by renesting within the same territory in which predation occurred (Rogers 1982). Daily visits (13:00–15:00) to 12 nests were made between 25 May and 5 June 1982. Nestlings, individually marked with fingernail polish, were weighed to the nearest estimated 0.1 g using a Pesola spring scale with 0.5-g increments. Between 15 April–16 June 1981 and 14 April–5 May 1982, I mist-netted a total of 65 breeding adults of both sexes (52 males, 13 females) on their territories and weighed them as above. Adults were sexed employing critiera of cloacal protuberance, incubation patch development, visible oviduct expansion, and territorial and courtship behavior. Growth rate (K) of nestlings was calculated using the graphical method (Ricklefs 1967).

I used an SPSS forward step-wise multiple regression (Nie et al. 1975) to relate environmental factors (independent variables) to the mass of 34 nestlings on day 7 (dependent variable, here taken to approximate fledgling mass). Independent variables are explained as follows. *Habitat* is a dummy variable with 0 ($n = 21$ nestlings from five nests) indicating territory and, therefore, nest location in the southern half of the study site at a lower elevation and in denser vegetation than the northern half. The dominant grass on the study site (*Digitari* sp.) grows to a seasonal maximum of 45–60 cm by August. Also common were red clover (*Trifolium pratense*) growing in numerous dense patches throughout the *Digitari,* and two species of wild mustard (Cruciferae), which were scattered loosely over the entire study area. Owing to its relatively lower elevation and location near one of the two large ponds, the southern half of that portion of the study site holding territories was distinctly more mesic and, consequently, harbored a more lush growth of the above plant species. While this distinction is subjective and not founded on quantitative measurements, the differences in vegetation between portions of the site were clearly observable. *Territory location* in the northern half of the study site was indicated by 1 ($n = 13$ nestlings from four nests). *Territory area* is the size of territory in m^2. *Hatching order* received a value of 1, 2, or 3, depending on when a nestling hatched relative to the first (1) occurrence of hatching in its nest. *Brood size* is the number of young hatching from a completed clutch, with *clutch size* equaling the number of eggs laid by a nesting female (cowbird eggs were absent from all study nests).

RESULTS

The form of the growth curve was logistic between days 0 through 8 of postnatal development (Fig. 1), as expected for a small passerine bird. A trend toward an asymptote was evident by day 7, after which growth slowed considerably (Fig. 1). Daily sample size diminished throughout the study, owing to predation on broods, until day 7 when many nestlings fledged. Four nestlings from the only brood remaining in the nest until day 9 were not weighed; this nest was empty on day 10.

The growth constant and related parameters calculated from Table 1 are (terminology and method of calculation after Ricklefs 1967): K = 0.620, t_{10-90} (time taken to complete growth between 10% and 90% of asymptotic weight) = 7.08 days, age at inflection = 3.40 days, *R* (asymptotic weight, here taken as day 7 weight, as a percent of breeding adult weight which equalled 19.26 g) = 80%. Asymptotic weight was 14.98 g (day 7 weight).

Habitat, hatching order, and day 0 mass yielded independent partial regression coefficients significantly different from zero, indicating a variety of influences on estimated fledgling body mass (Table 1). Territory area, brood size, and clutch size yielded nonsignificant regression coefficients (Table 1).

DISCUSSION

Slightly different corresponding values for growth parameters were reported earlier (Maher 1973) for a Saskatchewan population (K = 0.512, t_{10-90} = 8.6 days, age at inflection = 5.0 days, *R* = 93%, asymptotic weight = 16.0

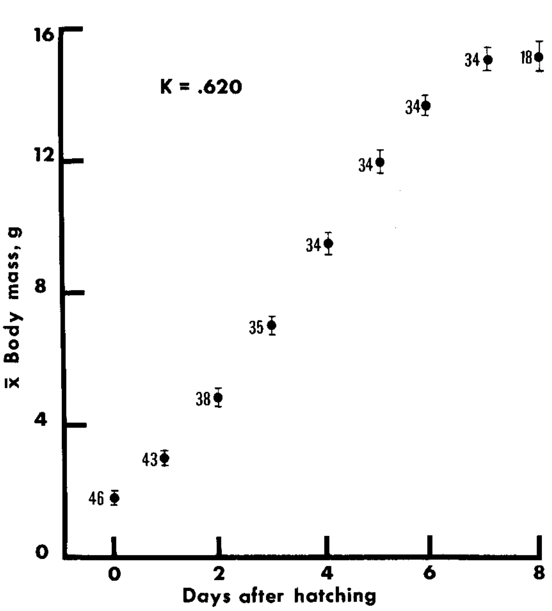

FIGURE 1. Relationship between mean body mass and days after hatching. Sample sizes are next to points indicating mean body mass, with lines indicating 1 SE. Day 0 is hatching day; K is Ricklefs' (1967) graphical K.

TABLE 1. Relationships of environmental and nest factors with day 7 weight in 34 central Michigan Savannah Sparrows from first broods of the breeding season. Factors are described in detail in the text. Cumulative R^2 for factors with significant (partial F-test) partial regression coefficient = 0.49. Territory area yielded a partial F value <0.001 and was eliminated from the regression equation by the SPSS program.

Factor	Partial regression coefficient (P)	R^2 contribution	Overall F (P)	Simple r
Habitat	1.72 (0.000)	0.20	8.23 (0.007)	0.45
Hatching (day 0) weight	2.17 (0.007)	0.16	8.91 (0.001)	0.24
Hatching order	−1.04 (0.031)	0.13	9.67 (0.000)	−0.36
Brood size	0.754 (0.072)	0.04	8.33 (0.000)	−0.08
Clutch size	−1.19 (0.213)	0.03	7.13 (0.000)	−0.24
Territory area	—	0.00	—	−0.20

g). In contrast to Maher, Ross (1980) reported an R value of 79% in the Ipswich Sparrow (*Passerculus sandwichensis princeps*), a Nova Scotia subspecies breeding on Sable Island. This is similar to the R value of the present study.

The R values reported for the Savannah Sparrow suggest a 7–21% range of post-nest-departure growth in contrast to the asymptote in Figure 1. If birds had been weighed after day 8, slight increases in body mass would have been detected over an unknown period during which parental feeding would likely continue, approximately two weeks in Nova Scotia (Ross 1980). Clearly, in both the Michigan and Nova Scotia populations the young leave the nest well before completing their growth, possibly an adaptation to reduce the probability of predation on nestlings (Ricklefs 1968). I noted no starvation of young, a finding also suggested by the low standard errors of daily weight means (Fig. 1).

The general habitat effect obtained in this study corroborates Ross (1980), who showed that nestlings raised in relatively dense habitat were heavier at day 7 than were nestlings raised in nearby, less vegetated habitat. I found an opposite effect of habitat sparseness as shown by the positive partial regression coefficient for habitat in Table 1. This effect may have been direct (e.g., the relatively sparse habitat allowed greater foraging efficiency than possible in relatively dense habitat), leading to greater food delivery and resultant growth rates in the former. Alternatively, the habitat effect may simply reflect selection of habitat types by fast- and slow-growing genotypes. The significance of day 0 mass as a factor indicates a slight tendency to maintain weight differences present at hatching throughout postnatal life. The significant hatching order factor suggests the presence of brood hierarchies, although this is an average result that may not have obtained in single nests.

In conclusion, both within- and among-population variation in growth parameters are indicated by results of this and other studies. Thus, growth in Savannah Sparrows appears to be adjusted to meet environmental constraints at local and geographic scales. Although my findings do not reveal the exact nature of relationships among the growth pattern and local and geographic environment, they suggest such relationships that can be involved in future studies.

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