GROWTH OF NESTLING IPSWICH SPARROWS IN RELATION TO SEASON, HABITAT, BROOD SIZE, AND PARENTAL AGE

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ABSTRACT.—At 7 days of age, nestling "Ipswich Sparrows" (*Passerculus sandwichensis princeps*) had attained 79% of the weight of breeding adults. Their weight at 7 days was uncorrelated ($r = 0.02$) with the exponential rate of weight gain during the period 0–7 days but negatively correlated ($r = -0.40$) with the rate at which this weight gain is damped. Nestling weight varied inversely with brood size and showed a midsummer minimum, especially with large brood sizes. Nestling tarsus length, growth rate, and damping rate each varied directly with brood size and had a midsummer maximum. Yearling adults raised nestlings with lower damping rates and higher weights than did older adults. Variation in nestling weight is thought to be influenced by sibling competition for food and the amount of time and energy invested by parents in nestlings at the expense of subsequent broods. The thermal consequences of brood size may contribute to the variation in tarsus length. *Received 2 August 1979, accepted 26 March 1980.*

THE weight and size of nestling birds has potential significance for their chances of survival (Perrins 1965) and the reproductive fitness of their parents. Here I attempt to describe the individual variation in the growth of nestling *Passerculus sandwichensis princeps* (recently designated a subspecies of the Savannah Sparrow, but hereafter called the Ipswich Sparrow) and to identify some of the causes of this variation.

Ipswich Sparrows are especially suitable for such study, as frequent disturbance of their nests on Sable Island, in the absence of terrestrial predators of any sort, does not greatly reduce nesting success. During this study, 0.75 nestlings left the nest per egg laid. A subsequent paper will examine the pattern of survivorship in young Ipswich Sparrows.

METHODS

The growth of nestling Ipswich Sparrows was measured during the summers of 1976, 1977, and 1978 on Sable Island, Nova Scotia as part of a study of the determinants of individual fitness. Ipswich Sparrows begin nesting in May and raise up to four consecutive broods, ending in late August or early September (Stobo and McLaren 1975). Often the age of one of the parents of the nestlings being studied was known from banding records. In the analysis, I assumed that the ages of a nestling's parents were uncorrelated, as there was no direct evidence to the contrary. Nestlings were studied in two major habitats, called Dense and Sparse. Dense habitat comprised grassy or heathy areas of well-consolidated terrain with representative plant species including bayberry (*Myrica pensylvanicus*), juniper (*Juniperus communis* and *J. horizontalis*), crowberry (*Empetrum nigrum*), meadow fescue (*Festuca rubra*), sedges (*Carex* spp.), and rushes (*Juncus* spp.). This habitat was usually in the vicinity of freshwater ponds. Sparse habitat, comprising the less consolidated sand dune areas, was vegetated almost entirely by various densities of marram grass (*Ammophila breviligulata*) and beach pea (*Lathyrus japonicus*). Although Sparse habitat lacked standing water, the vegetation was frequently wet from condensation and precipitation.

Nestlings were weighed daily between 1000 and 1400, from hatching until they were 7 days old

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(hatching = day 0). At hatching, individual nestlings were marked with colored thread tied around the leg, and at 7 days they were given an aluminum band. Nestlings were weighed with a spring scale to the nearest 0.5 g. The length of the right tarsus was measured to the nearest 0.1 mm with a vernier caliper when the nestlings were 7 days old. Nestlings discovered after hatching were weighed and measured when estimated by size and plumage to be 7 days old. Older nestlings were excluded, because broods break up and nestlings begin to leave the nest when 8 days old (Stobo and McLaren 1975: 45). The young birds fledge at approximately 3 weeks old, having spent about 2 weeks hiding in the grass.

The increase in weight of passerine nestlings is sigmoidal with time and may be described by the logistic equation (Ricklefs 1967). In my study, a least-squares method rather than the graphical method (Ricklefs 1967) was used to estimate the growth rates directly from the daily increments in nestling weight. For a similar method, see Crossner (1977). Because I did not know the final weight of each individual, I chose the first two coefficients of a polynomial regression to describe the trajectory of nestling growth. The difference equation,

$$\frac{\Delta W_i}{\Delta T_i} = r_a W_i - r_b W_i^2, \tag{1}$$

was used as an approximation to the logistic equation,

$$\frac{dW}{dT} = KW - \frac{K}{A}W^2. \tag{2}$$

W_i is the nestling weight on day i, beginning with day 0, and $\triangle W_i$ is the incremental change in weight ($W_{i+1} - W_i$) over the period $\triangle T_i$, which in this study was always 1 day. The logistic growth rate K (Ricklefs 1967) is here approximated by r_a, and the ratio K/A (growth rate/asymptotic weight) by r_b, which I will call the damping rate. Lack of equivalence between equations (1) and (2) occurs because of the problems of estimating the rate of exponential growth using interval measurements. Over a time interval of 1 day, equation (1) gives

$$\Delta W_i = r_a W_i - r_b W_i^2, \tag{3}$$

whereas the integrated form of equation (2) gives

$$\Delta W_i = \frac{(1 - e^{-K})(A - W_i)W_i}{W_i + (A - W_i)e^{-K}} \tag{4}$$

Equation (1) assumes parabolic growth within each discrete time interval. Equation (2) assumes linear growth only in an infinitesimally small increment of time and growth according to a dampened exponential function over any discrete time interval. Only when the time intervals become vanishingly small will equation (1) be exactly equal to the logistic equation. Consequently, my growth rate, r_a (with units of time^{-1}), is similar to but not identical to the logistic growth rate K. The damping rate, r_b, measures the rate at which the growth rate decelerates as the asymptote is approached. The ratio r_a/r_b is approximately equal to the asymptote A.

The rates r_a and r_b were estimated for each individual, using the curvilinear regression given by equation (1). Each individual was weighed eight times (days 0–7), providing seven points in the regression. If we let $W = X_1$, $W^2 = X_2$, and $\Delta W/\Delta T = Y$, then the least-squares estimators of r_a and r_b are

$$r_a = \frac{\Sigma X_1 Y - r_b \Sigma X_1 X_2}{\Sigma X_1^2} \tag{5}$$

$$r_b = \frac{\Sigma X_1 X_2 \Sigma X_1 Y - \Sigma X_1^2 \Sigma X_2 Y}{\Sigma X_1^2 \Sigma X_2^2 - (\Sigma X_1 X_2)^2}. \tag{6}$$

Four aspects of the growth of nestlings were analyzed; body weight at age 7 days, tarsus length at 7 days, growth rate (r_a), and damping rate (r_b). The general patterns of variation in these variables were investigated by four-way and five-way analyses of variance (ANOVA) with orthogonal design and fixed effects using the SPSS 7.0 computer package (Nie et al. 1975). First, each variable was compared among Years (1976–78), Months (June–August), Habitats (Dense, Sparse), and Brood Size (b/3–b/5). Nestlings were categorized according to the date when they were measured and banded at 7 days. Brood Size was defined as the number of nestlings in the brood during the second half of the nestling period. The uncommon broods of b/1 and b/2 were combined with b/3, and b/6 with b/5 in the analyses. Next, the parameter Parental Age (SY = second year, ASY = older) was included as the fifth main effect. The sample sizes were much smaller in the latter analyses because parental ages were often not known. SY adults were studied in both 1977 and 1978, while ASY adults were studied only in 1978.

TABLE 1. The weight (A) and tarsus length (B) of 7-day-old nestling Ipswich Sparrows subdivided according to natal habitat, brood size, and date of measurement. Variation in weight was analysed by ANOVA (Table 2). Values are mean ± SE g, with (*n*). All tarsus data were transformed to *z*-scores using the annual means and standard deviations. Variation in tarsus length was analyzed by ANOVA (Table 3). Values are mean ± SE; *n* is as in part A.

	Dense habitat				Sparse habitat				Monthly means			
Brood size:	b/3	b/4	b/5	Mean	b/3	b-4	b/5	Mean	b/3	b/4	b/5	Mean
A. Body weight												
June	20.3 ± 0.28 (39)	20.2 ± 0.17 (88)	20.4 ± 0.16 (92)	20.3 ± 0.11 (219)	20.8 ± 0.28 (22)	20.5 ± 0.23 (41)	19.7 ± 0.49 (5)	20.5 ± 0.17 (68)	20.5 ± 0.20 (61)	20.3 ± 0.14 (129)	20.4 ± 0.16 (97)	20.4 ± 0.09 (287)
July	21.1 ± 0.25 (44)	20.3 ± 0.15 (93)	19.8 ± 0.17 (150)	20.2 ± 0.11 (287)	20.9 ± 0.47 (13)	19.4 ± 0.24 (62)	19.4 ± 0.28 (59)	19.5 ± 0.18 (134)	21.0 ± 0.22 (57)	20.0 ± 0.14 (155)	19.7 ± 0.15 (209)	20.0 ± 0.10 (421)
August	20.7 ± 0.21 (63)	20.4 ± 0.20 (60)	19.8 ± 0.32 (25)	20.4 ± 0.14 (148)	20.4 ± 0.52 (19)	20.5 ± 0.32 (37)	20.7 ± 0.58 (5)	20.5 ± 0.25 (61)	20.7 ± 0.20 (82)	20.4 ± 0.17 (97)	19.9 ± 0.29 (30)	20.5 ± 0.12 (209)
Habitat means	20.7 ± 0.14 (146)	20.3 ± 0.10 (241)	20.0 ± 0.12 (267)	20.3 ± 0.07 (654)	20.7 ± 0.24 (54)	20.0 ± 0.16 (140)	19.5 ± 0.25 (69)	20.0 ± 0.12 (263)	20.7 ± 0.12 (200)	20.2 ± 0.09 (381)	19.9 ± 0.11 (336)	20.2 ± 0.06 (917)
B. Tarsus length												
June	−0.451 ± 0.177	0.050 ± 0.107	0.107 ± 0.096	−0.015 ± 0.068	−0.026 ± 0.246	−0.394 ± 0.141	0.078 ± 0.200	−0.240 ± 0.119	−0.297 ± 0.145	−0.091 ± 0.087	0.106 ± 0.092	−0.069 ± 0.059
July	0.180 ± 0.128	0.336 ± 0.081	0.088 ± 0.092	0.182 ± 0.058	−0.055 ± 0.255	−0.332 ± 0.137	0.006 ± 0.134	−0.156 ± 0.091	0.126 ± 0.114	0.069 ± 0.077	0.065 ± 0.076	0.075 ± 0.050
August	−0.300 ± 0.134	0.250 ± 0.079	−0.059 ± 0.154	−0.036 ± 0.073	−0.525 ± 0.224	0.015 ± 0.187	0.617 ± 0.084	−0.104 ± 0.139	−0.352 ± 0.115	0.160 ± 0.086	0.054 ± 0.137	−0.056 ± 0.066
Habitat means	−0.196 ± 0.086	0.210 ± 0.054	0.081 ± 0.063	0.067 ± 0.038	−0.208 ± 0.143	−0.258 ± 0.089	0.055 ± 0.117	−0.166 ± 0.064	−0.199 ± 0.074	0.038 ± 0.049	0.076 ± 0.055	0.000 ± 0.030

TABLE 2. Analysis of variance of the weight of 7-day-old nestling Ipswich Sparrows. The main effects in the analysis are year (YR) and month (MO) when measured, brood size (BS), and natal habitat (HB). F_1 was calculated using the residual mean square (R_1) after the extraction of all interaction terms. The sums of squares from the 3-way and 4-way interactions were added to residual R_1 to calculate R_2. F_2 was calculated using the more conservative residual R_2.

Source	df	Sum of squares	Mean square	F_1[a]	F_2[a]
Main effects	7	142.811	20.402	6.702***	6.578***
YR	2	26.187	13.094	4.301**	4.228*
MO	2	14.652	7.326	2.407ns	2.365ns
HB	1	21.214	21.214	6.969**	6.850**
BS	2	49.137	24.569	8.071***	7.932***
2-way interactions	18	121.887	6.772	2.224**	2.186**
YR × MO	4	28.441	7.110	2.336*	2.296ns
YR × HB	2	21.974	10.987	3.609*	3.547*
YR × BS	4	3.246	0.812	0.267ns	0.262ns
MO × HB	2	32.673	16.337	5.367**	5.275**
MO × BS	4	46.339	11.585	3.806**	3.740**
HB × BS	2	3.005	1.502	0.494ns	0.485ns
3-way interactions	20	92.039	4.602	1.512ns	
YR × MO × HB	4	42.382	10.596	3.481**	
YR × MO × BS	8	25.671	3.209	1.054ns	
YR × HB × BS	4	14.116	3.529	1.159ns	
MO × HB × BS	4	14.692	3.673	1.207ns	
4-way interaction					
YR × MO × HB × BS	4	28.304	7.076	2.324ns	
Residual R_1	867	2639.281	3.044		
Residual R_2	891	2759.623	3.097		
Total	916	3024.321			

[a] ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Some significant three-way and higher interaction terms occurred in the ANOVA's (Tables 2, 4, 6, and 8). Because these interactions are so difficult to interpret, however, their sums of squares were combined with the residual sum of squares (R_1) to form a new, larger residual (R_2). The F-ratios for the main effects and two-way interactions were recalculated using the larger residual mean square (R_2). The analyses will be discussed on the basis of the latter, more conservative set of F-ratios (F_2).

RESULTS

The weight of apparently newly hatched nestlings was approximately 2.0 g, but largely for practical reasons no special effort was made to determine the initial variation in body weight. The weight of 7-day-old nestlings [mean ± SE (n) = 20.2 ± 0.06 g (917)] was 83% of the weight of late-summer juveniles [24.3 ± 0.13 g (220)] and 79% of the weight of breeding adults [25.6 ± 0.55 g (108)] for sexes combined (from Stobo and McLaren 1975: 84).

The simple and first-order partial correlation coefficients were calculated for the three possible pairs of r_a (1), r_b (2), and weight at 7 days (3). Although weight was uncorrelated with r_a ($r_{12} = 0.021$, df = 590, $P > 0.05$) and negatively correlated with r_b ($r_{13} = -0.400$, df = 590, $P < 0.001$), the partial correlations ($r_{12.3} = 0.853$, df = 589, $P < 0.001$; $r_{13.2} = -0.878$, df = 589, $P < 0.001$) indicate that equation (1) adequately described weight gain up to 7 days. The growth and damping rates were highly correlated both in the simple ($r_{23} = 0.879$, df = 590, $P < 0.001$) and the partial ($r_{23.1} = 0.969$, df = 589, $P < 0.001$) correlations. This indicates very little variation in the ratio r_a/r_b, which is an estimate of the asymptote. Thus, when the growth rate r_a varies, it produces variation in the time required to reach the asymptote rather than in the asymptote itself.

TABLE 3. Analysis of variance of the tarsus length of 7-day-old nestling Ipswich Sparrows (Table 1B). See Table 2 for an explanation of the analysis.

Source	df	Sum of squares	Mean square	F_1[a]	F_2[a]
Main effects	7	25.464	3.638	4.033***	3.836***
YR	2	1.145	0.573	0.635ns	0.604ns
MO	2	3.697	1.848	2.049ns	1.949ns
HB	1	12.202	12.202	13.526***	12.867***
BS	2	9.579	4.790	5.309**	5.051**
2-way interactions	18	43.600	2.422	2.685***	2.554***
YR × MO	4	8.658	2.165	2.400*	2.283ns
YR × HB	2	1.698	0.849	0.941ns	0.895ns
YR × BS	4	7.220	1.805	2.001ns	1.903ns
MO × HB	2	2.196	1.098	1.217ns	1.158ns
MO × BS	4	10.940	2.735	3.032*	2.884*
HB × BS	2	11.971	5.985	6.635***	6.312**
3-way interactions	20	48.659	2.433	2.697***	
YR × MO × HB	4	14.132	3.533	3.917**	
YR × MO × BS	8	16.275	2.034	2.255*	
YR × HB × BS	4	12.936	3.234	3.585**	
MO × HB × BS	4	13.525	3.381	3.748**	
4-way interaction					
YR × MO × HB × BS	4	14.183	3.546	3.931**	
Residual R_1	867	782.096	0.902		
Residual R_2	891	844.937	0.948		
Total	916	914.001			

[a] ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** $P < 0.001$.

Nestling weight and tarsus length at 7 days and growth and damping rates for the period 0–7 days were compared, first among Years, Months, Habitats, and Brood Sizes, and then among these four parameters plus Parental Age. Although the Year terms in the ANOVA's were occasionally significant, they were generally ignored, because the sampling effort among the other parameters differed annually. Both the mean clutch size and mean brood size changed seasonally, with a peak in July. The seasonal changes in brood size are reflected in the sample sizes shown in Table 1.

The weight of 7-day nestlings is summarized in Table 1A. The four-way ANOVA of these data is given in Table 2. Nestlings from Dense habitat averaged 1% heavier than those raised in Sparse habitat. The mean weight of nestlings declined with increasing brood size. Nestlings raised in July were lighter than those from June or August, although the differences were not significant. The decline in nestling weight with increased brood size was slight in June, strong in July, and comparatively moderate in August. A significant interaction was also observed between Month and Habitat; the midsummer decline in weights was greater in Sparse habitat than in Dense.

At 7 days of age, nestling Ipswich Sparrows had a mean tarsus length [mean ± SE (n = 21.36 ± 0.037 mm (576); 1977 + 1978] that was 96% of the tarsus length of independent juveniles [22.43 ± 0.104 mm (35); 1977 only] and 95% of the adult tarsus length [22.49 ± 0.074 mm (82); sexes combined 1977 + 1978] as I measured them.

Early in the analysis I discovered that my method of measuring tarsus length had changed between 1976 and 1977. In 1976 I measured nestling tarsus lengths as having a mean ± SD (n) of 22.61 ± 1.00 mm (341). In 1977, however, it was 21.34

TABLE 4. The (A) growth rate r_a, and (B) damping rate r_b of 0–7-day-old nestling Ipswich Sparrows subdivided according to natal habitat, brood size, and date when 7 days old. See text for method of calculations of r_a and r_b. Variation in r_a and r_b was analysed by ANOVA (Tables 5 and 6). Values of r_a are means ± SE (n); values of r_b are (mean ± SE) × 10^{-2}, with n as in part A.

	Dense habitat				Sparse habitat				Monthly means			
Brood size:	b/3	b/4	b/5	Mean	b/3	b/4	b/5	Mean	b/3	b/4	b/5	Mean
					A. Growth rate, r_a							
June	0.659 ± 0.0126 (17)	0.649 ± 0.0121 (64)	0.626 ± 0.0105 (47)	0.642 ± 0.0074 (128)	0.617 ± 0.0113 (9)	0.561 ± 0.0395 (11)	0.618 ± 0.0147 (5)	0.593 ± 0.0185 (25)	0.645 ± 0.0098 (26)	0.636 ± 0.0123 (75)	0.625 ± 0.0096 (52)	0.634 ± 0.0070 (153)
July	0.628 ± 0.0195 (24)	0.675 ± 0.0107 (66)	0.652 ± 0.0086 (92)	0.657 ± 0.0064 (182)	0.594 ± 0.0364 (8)	0.630 ± 0.0200 (30)	0.659 ± 0.0108 (43)	0.642 ± 0.0101 (81)	0.619 ± 0.0171 (32)	0.661 ± 0.0098 (96)	0.654 ± 0.0068 (135)	0.652 ± 0.0054 (263)
August	0.625 ± 0.0096 (55)	0.664 ± 0.0113 (44)	0.625 ± 0.0198 (20)	0.640 ± 0.0071 (119)	0.615 ± 0.0187 (19)	0.620 ± 0.0135 (37)	0.622 ± 0.0142 (5)	0.618 ± 0.0100 (61)	0.623 ± 0.0085 (74)	0.644 ± 0.0090 (81)	0.624 ± 0.0160 (25)	0.632 ± 0.0058 (180)
Habitat means	0.632 ± 0.0077 (96)	0.663 ± 0.0069 (174)	0.641 ± 0.0064 (159)	0.648 ± 0.0040 (429)	0.611 ± 0.0128 (36)	0.615 ± 0.0115 (78)	0.652 ± 0.0091 (53)	0.626 ± 0.0068 (167)	0.626 ± 0.0066 (132)	0.648 ± 0.0060 (252)	0.644 ± 0.0053 (212)	0.642 ± 0.0035 (596)
					B. Damping rate, r_b							
June	2.97 ± 0.121	3.05 ± 0.090	2.85 ± 0.076	2.97 ± 0.055	2.63 ± 0.088	2.14 ± 0.286	2.98 ± 0.095	2.48 ± 0.144	2.85 ± 0.090	2.92 ± 0.094	2.86 ± 0.069	2.89 ± 0.054
July	2.75 ± 0.167	3.22 ± 0.071	3.15 ± 0.075	3.13 ± 0.052	2.35 ± 0.290	3.09 ± 0.149	3.15 ± 0.079	3.05 ± 0.078	2.65 ± 0.146	3.18 ± 0.067	3.15 ± 0.057	3.10 ± 0.043
August	2.78 ± 0.076	3.12 ± 0.068	2.99 ± 0.128	2.94 ± 0.050	2.73 ± 0.151	2.79 ± 0.090	2.84 ± 0.158	2.77 ± 0.072	2.77 ± 0.068	2.97 ± 0.058	2.96 ± 0.107	2.88 ± 0.041
Habitat means	2.81 ± 0.064	3.13 ± 0.046	3.04 ± 0.052	3.03 ± 0.031	2.62 ± 0.105	2.81 ± 0.088	3.10 ± 0.067	2.87 ± 0.053	2.76 ± 0.055	3.03 ± 0.043	3.06 ± 0.043	2.98 ± 0.027

TABLE 5. Analysis of variance of the growth rate r_a of nestling Ipswich Sparrows (Table 4A). See Table 2 for an explanation of the analysis.

Source	df	Sum of squares	Mean square	F_1[a]	F_2[a]
Main effects	7	23.482 (× 10^{-2})	3.355 (× 10^{-2})	5.466***	5.073***
YR	2	7.579	3.789	6.174**	5.730**
MO	2	4.317	2.158	3.517*	3.264*
HB	1	9.636	9.636	15.699***	14.570***
BS	2	5.770	2.885	4.700**	4.362**
2-way interactions	18	32.908	1.828	2.979***	2.765***
YR × MO	4	5.288	1.322	2.154ns	1.999ns
YR × HB	2	2.790	1.395	2.273ns	2.110ns
YR × BS	4	12.637	3.159	5.147***	4.777***
MO × HB	2	0.325	0.163	0.265ns	0.246ns
MO × BS	4	1.754	0.439	0.715ns	0.663ns
HB × BS	2	7.733	3.866	6.300**	5.847**
3-way interactions	18	36.393	2.022	3.394***	
YR × MO × HB	3	4.136	1.379	2.246ns	
YR × MO × BS	7	19.393	2.770	4.514***	
YR × HB × BS	4	6.502	1.626	2.649*	
MO × HB × BS	4	2.886	0.721	1.176ns	
4-way interaction					
YR × MO × HB × BS	1	2.376	2.376	3.871*	
Residual R_1	551	338.178	0.614		
Residual R_2	570	376.947	0.661		
Total	595	433.336			

[a] ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

± 0.80 mm (336), and in 1978 in was 21.38 ± 0.97 mm (240). This was corrected by transforming all tarsus lengths by the z-transformation (Sokal and Rohlf 1969), using the annual means and standard deviations. This necessarily made the Year term in the ANOVA nonsignificant.

The pattern of variation in tarsus length (Tables 1B and 3) was complex and very different from that observed for nestling weight. As with nestling weight, tarsus length was greater for nestlings raised in Dense habitat than for those in Sparse habitat. Nestling tarsus length was greater for nestlings raised in July, however, than for those raised in June or August (not significantly so), and mean tarsus length increased with increasing brood size. A significant interaction was observed between Habitat and Brood Size, but in each habitat broods of three had the smallest (or nearly so) tarsus lengths.

Very similar trends were observed for growth rate r_a (Tables 4A and 5), and damping rate r_b (Tables 4B and 6), as one might expect from the strong positive correlation between them. For both of these rates, nestlings from Dense habitat had larger mean values than those from Sparse habitat; means were largest in July, and in the three brood sizes the smallest mean rates were in broods of three. Very similar interactions between Habitat and Brood Size were found for both r_a and r_b.

The marginal totals in Tables 1B, 4A, and 4B show that the trends in nestling tarsus length are very similar to those in growth and damping rates. In contrast, the trends in nestling weight are different from, and generally the converse of, those found for growth and damping rates.

The size and growth of Ipswich Sparrow nestlings varied in an unpredicted manner with respect to parental age. The improvement in parental abilities expected to

TABLE 6. Analysis of variance of the damping rate r_b of nestling Ipswich Sparrows (Table 4B). See Table 2 for an explanation of the analysis.

Source	df	Sum of squares	Mean square	F_1[a]	F_2[a]
Main effects	7	18.960 (× 10^{-4})	2.709 (× 10^{-4})	7.162***	6.928***
YR	2	1.794	0.897	2.372ns	2.294ns
MO	2	4.861	2.430	6.426**	6.216**
HB	1	5.001	5.001	13.224***	12.791***
BS	2	7.708	3.854	10.191***	9.858***
2-way interactions	18	15.849	0.880	2.328**	2.252**
YR × MO	4	1.597	0.399	1.056ns	1.021ns
YR × HB	2	0.057	0.028	0.075ns	0.072ns
YR × BS	4	6.292	1.573	4.159**	4.023**
MO × HB	2	1.200	0.600	1.587ns	1.535ns
MO × BS	4	1.374	0.343	0.908ns	0.878ns
HB × BS	2	2.671	1.336	3.531*	3.416*
3-way interactions	18	14.384	0.799	2.113**	
YR × MO × HB	3	1.336	0.445	1.178ns	
YR × MO × BS	7	7.038	1.005	2.658*	
YR × HB × BS	4	1.733	0.433	1.146ns	
MO × HB × BS	4	2.327	0.582	1.538ns	
4-way interaction					
YR × MO × HB × BS	1	0.088	0.088	0.232ns	
Residual R_1	551	208.387	0.378		
Residual R_2	570	222.859	0.391		
Total	595	257.668			

[a] ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

accompany increased age did not result in larger or more quickly growing nestlings. The offspring of both male and female ASY adults averaged lighter than those of younger adults, especially at the largest brood size (Table 7). For both parental sexes, a significant Age by Month interaction occurred when the mean weight of nestlings raised by SY parents declined as the summer progressed, whereas the offspring of ASY parents were lightest in July. This interaction may have occurred because the broods of ASY parents were largest in July (Ross 1979). These weight differences were not paralleled by differences in the tarsus length of the offspring of SY and ASY adults. Significant interactions in tarsus length, however, were found for both Age by Brood Size and Age by Month among female parents. The biological meaningfulness of these interactions is reduced because of the lumping of heterogeneous subsets resulting from the limitations of the sampling effort and from the larger clutches and earlier nesting of ASY adults (Ross 1979). The growth rates of nestlings raised by males or females of either age did not differ significantly. In contrast, the damping rates of nestlings raised by ASY adults were significantly greater than those of nestlings raised by SY males or females. In summary, the nestlings of ASY adults began to grow as quickly as those of SY adults, but their weight gain was curtailed sooner, resulting in lower body weight at age 7 days.

DISCUSSION

The growth rate r_a is clearly a measure of the rate of increase in biomass. Although r_a is not identical to the logistic growth rate K of Ricklefs (1967), the two are positively correlated. The damping rate r_b is much less easy to interpret, because its units ($\text{weight}^{-1} \cdot \text{time}^{-1}$) do not have any simple biological interpretation. Because

TABLE 7. Mean ± SE (n) values for four nestling growth parameters for nestling Ipswich Sparrows subdivided according to the known age of a parent. The given probabilities are for the differences between age groups within sexes from a larger ANOVA. See text for definitions.

Parental sex	Parental age	7-day nestling weight (g)[a]	7-day nestling tarsus length (z)[a]	Growth rate, r_a	Damping rate, r_b ($\times 10^{-2}$)[a]
Male	SY	20.8*** ± 0.13 (164)	0.194ns ± 0.078 (164)	0.637ns ± 0.0074 (108)	2.88* ± 0.053 (108)
Male	ASY	19.2 ± 0.25 (82)	0.105 ± 0.134 (81)	0.635 ± 0.0100 (62)	3.02 ± 0.071 (62)
Female	SY	20.5** ± 0.14 (145)	−0.071ns ± 0.082 (145)	0.640ns ± 0.0077 (125)	2.95*** ± 0.062 (125)
Female	ASY	20.1 ± 0.24 (76)	0.088 ± 0.107 (76)	0.637 ± 0.0093 (68)	3.05 ± 0.061 (68)

[a] ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** $P < 0.001$.

r_b is the coefficient of the squared term in equation (1), variation in r_b would indicate greater variation in the second half of the growth trajectory than in the first. The damping rate measures the rate at which the instantaneous growth rate decreases as the asymptote is approached and therefore may indicate the rate at which energy is diverted from simple biomass accumulation to tissue differentiation.

A lack of a positive correlation between the growth rate and the asymptotic or near-asymptotic weight is widely found in studies of passerines. Growth rates presented by or calculated from Ricklefs (1968, and pers. comm.), Hussell (1972), Dyrcz (1974), Crawford (1977), and Crossner (1977) all fail to show distinct trends. Ricklefs (pers. comm.) has indicated that there may be no inherent relationship between the growth rate and asymptotic weight of nestling Starlings (*Sturnus vulgaris*), but positive correlations may arise between the two in each nutritional situation. Thus Ricklefs' K and my r_a may not be adequate indices of the overall quality of a nestling's existence unless they are set in a larger framework.

The trends observed in weight and tarsus length may result from certain aspects of the nestlings' nutritional and thermal environment. The decrease in nestling weight in larger brood sizes (Table 1A) probably reflects the well-known problem of sibling competition for a food source limited by the parental foraging abilities (Royama 1966, Seel 1970, Hussell 1972, Askenmo 1977, Schifferli 1978). Because nestling weights were higher in the Dense habitat than in the Sparse habitat for broods of four and five, especially in July when over half of the young from Sparse habitat were raised, a slight amount of the variation in nestling weight may be attributable to differences in food availability between the habitats.

Newly hatched nestlings are poikilothermic, gradually achieving homoiothermy near the end of the nest period as they develop the plumage and physiological mechanisms required for thermoregulation (Dawson and Evans 1957, 1960; O'Connor 1975a,b). Because the rate of heat loss depends on the surface/volume ratio of the brood and is correlated with brood size (O'Connor 1975b), nestlings will be more prone to hypothermia at lower brood sizes. Temperature directly modifies the rate of bone growth by influencing both arterial dilation and metabolic rates (Brookes and May 1972). Skeletal development in the limbs and tail of white mice

(*Mus musculus*) is much more sensitive to environmental temperature than is thoracic skeletal development (Garrard et al. 1974). Consequently, the overall trend for tarsus length to increase in larger broods (Table 1B) may result from brood size-dependent variation in the nestlings' body temperature. The significant Month by Brood Size interaction (Table 3) may have arisen because July was a warmer, sunnier month than June, whereas nests were more shaded under tall grass in August.

Variation in the growth rate (Table 4A) and the damping rate (Table 4B) may be due to both nutritional and thermal factors. Each nestling in a large brood would receive a smaller share of food than in a smaller brood, but improved thermal conditions would mean that less energy was expended on thermogenesis. July may be both the warmest and most food-rich month, and such conditions could produce faster growth and development.

In many passerine species older male and female parents have improved reproductive performance through a combination of increased reproductive effort and increased parental success (Klomp 1970, Perrins and Moss 1974, Rheinwald et al. 1976, Crawford 1977, De Steven 1978, Harvey et al. 1979, Ross 1979). Although it is commonly assumed that the foraging abilities of passerines improve with age (e.g. Lack 1968: 297), such an improvement has been demonstrated only for non-passerines (Orians 1969, Recher and Recher 1969, Buckley and Buckley 1974, Groves 1978). Crawford (1977) found that both yearling Red-winged (*Agelaius phoeniceus*) and Yellow-headed (*Xanthocephalus xanthocephalus*) blackbirds raised lighter nestlings than did older adults. Growth and damping rates that I calculated from the mean trajectories of weight gain for both species were larger for the offspring of yearlings. Thus age-related changes in the parental skills of passerines seem likely.

Table 7 suggests that ASY Ipswich Sparrows do not provide a greater quality of parental care than do SY birds but actually reduce the amount of food delivered to their nestlings. Stobo and McLaren (1975) found that late in the nestling period the female Ipswich Sparrow reduces her attendance at the present brood and produces a subsequent nest and clutch of eggs before the independence of the former nestlings. Throughout the nestling period, the male increases his rate of food delivery and takes a major share in the care of the young after they leave the nest. By this division of labor, a pair of Ipswich Sparrows may raise up to four broods in a summer.

I found that when either of the parents was SY in age, more time was taken to produce the next nest and clutch after the previous brood had been successfully raised to 7 days than when either parent was ASY (Ross 1979). In contrast, there was no significant difference between the parental age classes in the time required to renest and relay after the clutch or brood was predated or abandoned. This suggests that the age effect relates to the willingness of an individual female to begin the next clutch or of an individual male to take greater responsibility for the brood in progress, rather than to differences in sexual competence or egg formation. These age differences contributed to a greater production of eggs and 7-day-old nestlings by ASY adults than by SY adults in a summer (Ross 1979).

The probability of survival of young Great Tits (*Parus major*) is correlated with their weight at fledging (Perrins 1965). Therefore, the lower weights of the nestlings raised by ASY Ipswich Sparrows would seem maladaptive. The probability that an individual would return to Sable Island (the sole breeding place of the Ipswich Sparrow) at age SY, however, was independent of the nestling's weight, tarsus length, r_a, r_b, habitat, date of hatching, brood size, or parental age during 1976–78 (Ross and McLaren, in prep.). After they leave the nest, young Ipswich Sparrows spend approximately 2 weeks hiding in the grass before they achieve independence from their parents. This period may allow them enough compensatory feeding to shore up their half of the parent-offspring conflict (Trivers 1974). Adults certainly benefit if they can increase the number of offspring by reducing the care of each to the barest minimum. Differences in nestling weight related to parental age probably reflected modifications to the parents' allocations of energy to offspring in an attempt to increase parental fitness.

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LITERATURE CITED

ASKENMO, C. 1977. Effects of addition and removal of nestlings on nestling weight, nestling survival, and female weight loss in the Pied Flycatcher *Ficedula hypoleuca* (Pallas). Ornis Scandinavica 8: 1–8.

BROOKES, M., & K. U. MAY. 1972. The influence of temperature on bone growth in the chick. J. Anat. 111: 351–363.

BUCKLEY, F. G., & P. A. BUCKLEY. 1974. Comparative feeding ecology of wintering adult and juvenile Royal Terns (Aves: Laridae, Sterninae). Ecology 55: 1053–1063.

CRAWFORD, R. D. 1977. Breeding biology of year-old and older female Red-winged and Yellow-headed blackbirds. Wilson Bull. 89: 73–80.

CROSSNER, K. A. 1977. Natural selection and clutch size in the European Starling. Ecology 58: 885–892.

DAWSON, W. R., & F. C. EVANS. 1957. Relation of growth and development to temperature regulation in nestling Field and Chipping sparrows. Physiol. Zool. 30: 315–327.

———, & ———. 1960. Relation of growth and development to temperature regulation in nestling Vesper Sparrows. Condor 62: 329–340.

DE STEVEN, D. 1978. The influence of age on the breeding biology of the Tree Swallow *Iridoprocne bicolor*. Ibis 120: 516–523.

DYRCZ, A. 1974. Factors affecting the growth rate of nestling Great Reed Warblers and Reed Warblers at Milicz, Poland. Ibis 116: 330–339.

GARRARD, G., G. A. HARRISON, & J. S. WEINER. 1974. Genotypic differences in the ossification of 12 day old mice at 23°C and 32°C. J. Anat. 117: 531–539.

GROVES, S. 1978. Age-related differences in Ruddy Turnstone foraging and aggressive behavior. Auk 95: 95–103.

HARVEY, P. H., P. J. GREENWOOD, C. M. PERRINS, & A. R. MARTIN. 1979. Breeding success of Great Tits *Parus major* in relation to age of male and female parent. Ibis 121: 216–219.

HUSSELL, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42: 317–364.

KLOMP, H. 1970. The determination of clutch-size in birds: a review. Ardea 58: 1–124.

LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, & D. H. BENT. 1975. SPSS: statistical package for the social sciences, 2nd Ed. New York, McGraw-Hill.

O'CONNOR, R. J. 1975a. Growth and metabolism in nestling passerines. Symp. Zool. Soc. London 35: 277–306.

———. 1975b. The influence of brood size upon metabolic rate and body temperature in nestling Blue Tits *Parus caeruleus* and House Sparrows *Passer domesticus*. J. Zool., London 175: 391–403.

ORIANS, G. 1969. Age and hunting success in the Brown Pelican. Anim. Behav. 17: 316–319.

PERRINS, C. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major* L. J. Anim. Ecol. 34: 601–647.

———, & D. MOSS. 1975. Reproductive rates in the Great Tit. J. Anim. Ecol. 44: 695–706.

RECHER, H., & J. RECHER. 1969. Comparative foraging efficiency of adult and immature Little Blue Heron (*Florida caerulea*). Anim. Behav. 17: 320–322.

RHEINWALD, G., H. GUTSCHER, & K. HÖRMEYER. 1976. Einfluss des Alters der Mehlschwalbe (*Delichon urbica*) auf ihre Brut. Vogelwarte 28: 190–206.

RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48: 978–983.

———. 1968. Patterns of growth in birds. Ibis 110: 419–451.

ROSS, H. A. 1979. Determinants of fitness in the Ipswich Sparrow. Unpublished Ph.D. dissertation, Halifax, Nova Scotia, Dalhousie Univ.

ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits, *Parus major*. Ibis 108: 313–347.

SCHIFFERLI, L. 1978. Experimental modification of brood size among House Sparrows *Passer domesticus*. Ibis 120: 365–369.

SEEL, D. C. 1970. Nestling survival and nestling weights in the House Sparrow and Tree Sparrow *Passer* spp. at Oxford. Ibis 112: 1–14.

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman.

STOBO, W. T., & I. A. MCLAREN. 1975. The Ipswich Sparrow. Proc. Nova Scotian Inst. Sci. 27, Suppl. 2: 1–105.

TRIVERS, R. L. 1974. Parent-offspring conflict. Amer. Zool. 14: 249–264.