INITIAL SIZE AND SUBSEQUENT GROWTH
IN PASSERINE NESTLINGS

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INTRODUCTION

Studies of several different species have suggested that chicks hatching from large eggs grow faster and possibly survive better than do young from smaller eggs (Skogland et al., 1952; Parsons, 1970; Schifferli, 1973). Such effects could arise if chicks hatching from the larger eggs were larger in body-size (i.e. more advanced in development at hatching, and thus able to fledge earlier). Alternatively, the larger egg might provide a chick with more reserves at hatching, an advantage of particular value if food were scarce during the nestling period. The present study compares the effects of early size on subsequent growth in three species of small passerines—Blue Tit (*Parus caeruleus*), House Martin (*Delichon urbica*), and House Sparrow (*Passer domesticus*).

MATERIALS AND METHODS

Nestlings of each species were studied near Oxford, England, during the summers of 1970 and 1971. Blue Tit and House Sparrow data were obtained from young in nestboxes, but all House Martin young examined were in natural nests in the eaves of farm buildings. Nests were visited daily until the eggs hatched, thus establishing nestling ages: sparrows were visited daily thereafter, titmice daily through day 7 (day 0 = day of hatching) and at either 24- or 48-hour intervals subsequently, and swallow young were visited at two-day intervals. Body weight and wing length were recorded for the individually marked young at each visit; tarsus length was additionally recorded for each chick on the hatching day. Sample sizes for the present analyses were 48 Blue Tits, 55 House Martins, and 15 House Sparrows.

This study formed part of a wider study of nestling growth (O'Connor, 1975 a-c and in press) and further details of study methods and of related aspects of the growth of the young are presented in these references.

RESULTS

In the present study early size is assessed as weight on day 0, the day of hatching. For young visited at 24-hour intervals these weights correspond to an average age of 12 hours rather than to strict hatching weights; this approximation is adequate here (see below). Within this approximation differences in day 0 weights reflect differences in egg weights; Jones (1973) and Schifferli (1973) have shown that egg weights and hatching weights are strongly linearly correlated, both inter- and intra-specifically.

A spread in day 0 weights over a sample of nestlings can in principle be due to any of three effects: (1) the chicks hatched at more or less the same time but with different levels of lipid re-

serves, (2) the chicks hatched at similar weights but at different
times since the eggs were inspected 24 hours earlier, so that the
observed variation at first weighing reflects the differences in
postembryonic growth of chicks fed over periods ranging from 0
to 24 hours, or (3) the chicks differ in overall size at hatching,
presumably as a result of differences in egg size.   Before I can
validly use day 0 weights as measures of early size for the present
study it is necessary to preclude the two alternative explanations
of day 0 weight variation.

<div align="center">TABLE 1.</div>

Correlations between parameters of nestling size on the day of hatching

| | Correlation[1] of wing length with | | |
Species	Body weight	Tarsus length	Sample size
Blue Tit	0.845[2]	0.666	48
House Martin	0.373	0.468	55
House Sparrow	0.948	0.824	15

[1]All correlations were significant at $P < 0.01$ or better.
[2]Calculated for 126 nestlings, i.e. including some not studied beyond day 0.

Weight and wing length and wing length and tarsus length
were correlated in day 0 chicks of all three species (Table 1); day
0 weights can therefore probably be regarded as measures of size
rather than as measures of lipid reserves *per se* since it is unlikely
that lipid content and skeletal size should vary independently but
in parallel. If this variation in day 0 size is due to variation in the
time lapsed since hatching rather than to variation in egg size,
then a regression of weight on wing length within day 0 should
describe the relationship of these two size measures to each other
during the first 24 hours of growth.   This relationship can be
compared against an equivalent measure of "true" growth, namely,
the weight change between day 0 and day 1 divided by the cor-
responding change in wing length (Table 2), since we know that
these changes are due to growth over 24 hours.   To allow for the
possibility of non-linear growth, regressions of weight on wing
length were also calculated for the day 1 data.   For Blue Tit and
House Martin the results were unequivocal (Table 2): the weight-
wing length gradient for the overnight day 0 to day 1 period was
considerably in excess of the regression slopes calculated within
either day alone, implying the presence of size distribution in these
species at hatching.   For House Sparrow, however, it was not
possible to preclude the possibility of a spread in hatching times
on the basis of this analysis alone.   However, an analysis of re-
gressions of day n weights on day 0 weights in Table 3 shows for
House Sparrow that the regression slope increased with age over
the first week of the development period.   If a spread in hatching
times lay behind the observed variation in day 0 weights, such an

<div align="center">TABLE 2.</div>

Comparison of weight-wing length regression slopes with a known growth gradient

	Blue Tit	House Martin	House Sparrow
Regression[1] of weight on wing length: day 0	0.46 ± 0.04	0.40 ± 0.14	1.59 ± 0.15
Growth gradient[2] between day 0 and day 1	0.77	1.22	1.56
Regression[1] of weight on wing length: day 1	0.50 ± 0.04	0.68 ± 0.13	1.42 ± 0.20

[1]Slope of a regression of body weights on the corresponding wing lengths within the age group with standard deviation, in g/mm.
[2]Calculated as change in mean weight between day 0 and day 1 divided by change in mean wing length, as g/mm.

increase could be attributed to increase in absolute growth rate with age during early development (Ricklefs, 1968c), but in practice the correlation between absolute growth rates and the corresponding regression slopes was poor ($r = 0.051$, non-significant) and thus inconsistent with the hatching spread argument. Similarly, the increase in regression slope with age in Blue Tit was correlated with an increase in absolute growth rate at only $r = 0.262$ (non-significant), agreeing with the other results (Table 2) indicating that day 0 weight variation represents primarily a size spread rather than a time spread at hatching.

The relationship between day 0 weight and subsequent growth was assessed for each species by computing for each age the correlation coefficient between the weight of each nestling at that age and its weight on day 0; these coefficients are plotted as a function of age in Figure 1. For House Martins only day 2 weights were statistically correlated with the initial weight, but in the other species weights over the first seven days were closely related to early weight, with 60-65% ($100 \ r^2$) of the statistical variation in body weight determined by the day 0 weight. Except in House Martins the correlations for older birds declined with age towards negative values, this attaining statistical significance for day 18 Blue Tits. This trend indicates that the enhancement effects of early size on body weight (but not necessarily on development; see below) decreased with age. In House Martins the correlation of weight with day 0 size decreased significantly between day 2 and day 7 (Runs test, $P < 0.05$) and varied irregularly thereafter; any size effects in House Martins were thus both small and short-lived. This difference from the other two species parallels the rather low dispersion of day 0 weights in the House Martin (coefficient of variation = 14.0%) compared with those of the other species (Blue Tit 20.0%, House Sparrow 30.0%).

The results in Figure 1 show only the extent to which covariation of later weights with day 0 weights occurs. They do not reveal the magnitude of the weight difference between two chicks on day n as a result of a difference in their day 0 weights. This was examined by tabulating the regression coefficients for each age group of nestlings in relation to age (Table 3); coefficients for

TABLE 3.

Regression coefficients for regressions of day n weights on day 0 weights

Age (day n)	Blue Tit		House Sparrow	
	Slope[1]	SD	Slope[1]	SD
1	1.02	0.09	1.00	0.14
2	0.94	0.16	1.13	0.28
3	1.82	0.17	1.40	0.27
4	1.79	0.26	2.06	0.33
5	1.93	0.29	1.68	0.42
6	0.15	0.40	2.27	0.37
7	2.05	0.38	1.78	0.56
8	0.90	0.65	0.60	0.30
9	0.00	0.25	0.37	0.33
10	0.19	0.66	−0.06	0.42
11	−0.35	0.24	−0.24	0.46
12	−0.25	0.52	−0.26	0.25
13	−0.35	0.30	−0.09	0.24
14	−0.46	0.41	−0.01	0.24
15	−0.56	0.26	Most birds fledged	
16	−0.62	0.42		
17	−0.29	0.19		
18	−1.99	0.87		
19	−0.06	0.16		
20	Most birds fledged			

[1]The regression slope has units g weight on day n/g weight on day 0.

House Martin were not calculated since the correlations for this species (Fig. 1) were so low (Snedecor and Cochran, 1967). The data show that in Blue Tits any weight difference present on day 0 was maintained unchanged through the first 48 hours of growth but was then almost doubled ($t = 4.76$, $P < 0.001$) and maintained for the next five days before decreasing sharply. In House Sparrow young, by contrast, weight differences between chicks systematically increased with age over the first week ($r = 0.806$, $P < 0.05$) but then fell sharply. These patterns are illustrated in Figure 2, in which the growth curve of 1971 sparrow chicks of greater than average day 0 weight is compared with that of chicks of below average day 0 weight. The "weight recession" (Edson, 1930)
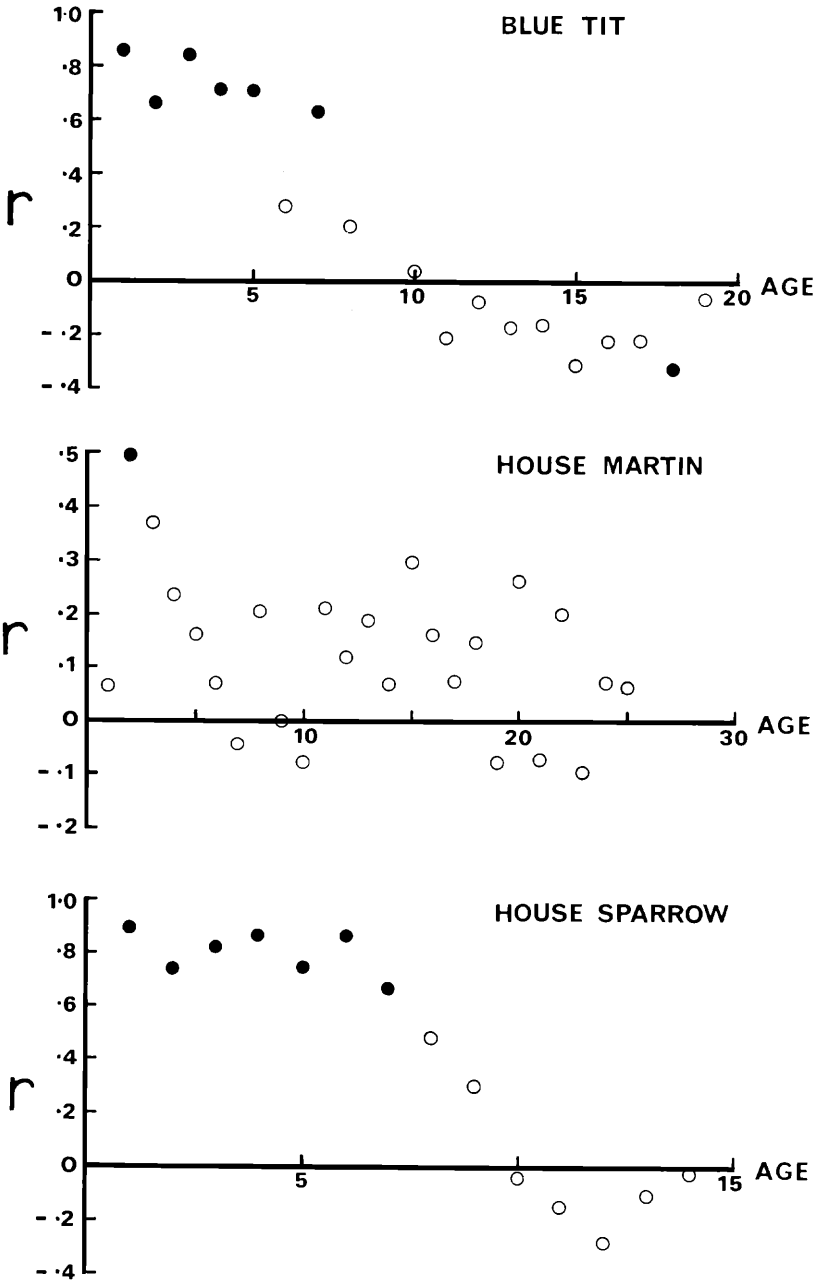
FIGURE 1. Age change in the correlation of body weight with weight on the day of hatching. Solid points indicate the correlation was significant at $P < 0.05$.

apparent in these curves occurs in all three species (O'Connor, 1975a) and is thought to be associated with arboreal or aerial feeding patterns (Ricklefs, 1968a). The crossing-over of the weight curves of young of different day 0 weights accounts for the decline in regression coefficients (Table 3).

Growth curves involving weight recession can be characterized by a *maximum weight* and by an *age of maximum weight*. In addition we can specify a *fledging weight* and a *fledging age*, the former being defined in practice as the last weight recorded for the nestling concerned. These variables are of interest because they can vary independently of age for individual young: e.g. two young at a given age might have identical weights yet one have passed, and the other be yet approaching, their respective maximum weights. The effects of early size on these variables are summarized in Table 4. Neither maximum weights nor fledging weights were

TABLE 4.

Effect of nestling weight on the day of hatching on some parameters of subsequent growth.

Growth parameter[1]	Correlation with hatching day weight in		
	Blue Tit	House Sparrow	House Martin
Maximum weight as nestling	0.114	0.143	0.228
Fledging weight	0.045	0.357	0.071
Age of maximum weight	−0.430**	−0.797**	−0.181
Age of fledging	−0.102	−0.833**	−0.114
Wing length at fledging	0.511*	−0.608*	−0.067

[1]Fledging data estimated as the data on the last day on which the nestling was present in the nest.

*$P < 0.05$ **$P < 0.01$

affected by day 0 weight, but in both Blue Tits and House Sparrows those chicks that were heavy on day 0 reached their maximum weights sooner than did lighter chicks. In addition, initially heavy sparrow chicks fledged early. These results suggest therefore that the net effect of increased day 0 weight was to accelerate the chick's progress along an otherwise determinate growth curve.

The final line of Table 4 shows the effects of day 0 weight upon the wing length of fledglings (again approximated by the last measurement recorded for each nestling). In Blue Tits heavy day 0 weight resulted in longer wing length but in the House Sparrow this trend was reversed. No effect was present in House Martins. These results were unexpected, because one would predict *a priori* that accelerated weight growth would be paralleled by accelerated feather growth in all three species. The possibility that feather growth was affected by the level of weight attained at a given

age was therefore tested by computing partial correlation co-efficients between weight, wing length, and age at fledging (Table 5). These showed that nestlings fledging at a given weight had longer wings the longer their time in the nest and that young

TABLE 5.

Partial correlations among fledging variables.

Fledging variable			Species		
Pair in correlation		Constant	Blue Tit	House Martin	House Sparrow
Wing	Age	Weight	0.428**	0.694**	0.941**
Weight	Age	Wing	−0.547**	−0.395	−0.602*
Weight	Wing	Age	0.237	0.243	0.551

*$P < 0.05$ **$P < 0.01$

fledging with a specified wing length were lighter if they had spent longer as nestlings. No relationship was found between wing length and weight independently of age except perhaps in the House Sparrow, in which heavier fledglings tended to have longer wings ($r = 0.551$, one-tailed $P = 0.032$). This effect accounted for the discrepancy in Table 4, for when I took it into consideration by calculating the day 0 weight effects as partial correlations, I found that heavy day 0 sparrows had longer wings at fledging when corrected for nestling period ($r_p = 0.683$, $P < 0.05$). In addition the effect of day 0 weight on nestling period was independent both of wing length at fledging ($r_p = 0.861$, $P < 0.01$) and of the age at which the chick had attained its maximum weight ($r_p = -0.692$, $P < 0.05$). In summary, therefore, the effects of increased day 0 size were to allow young Blue Tits and House Sparrows to reach their maximum weights as nestlings early and to fledge with better developed flight feathers. Initially heavy sparrows also fledged early.

DISCUSSION

It is generally assumed in avian growth studies that rates of weight increase are equivalent to rates of development (see review by Ricklefs, 1968c). The results presented here show, however, that this assumption is not valid for species exhibiting weight recession - individuals with greater day 0 weights showed positive weight increments prior to attaining peak weights but negative weight increments at older ages. That is, these chicks gained weight faster at first but lost it faster subsequently (Figs. 1, 2). Moreover, the larger day 0 weights were correlated with greater wing and tarsal development on day 0 (Table 1) and with greater develop-ment of the primary feathers at the end of the nestling period (Table 4), which features suggest that development was indeed faster in such birds. If so, the loss of weight shown in Figure 2 must represent an integral part of the development process of
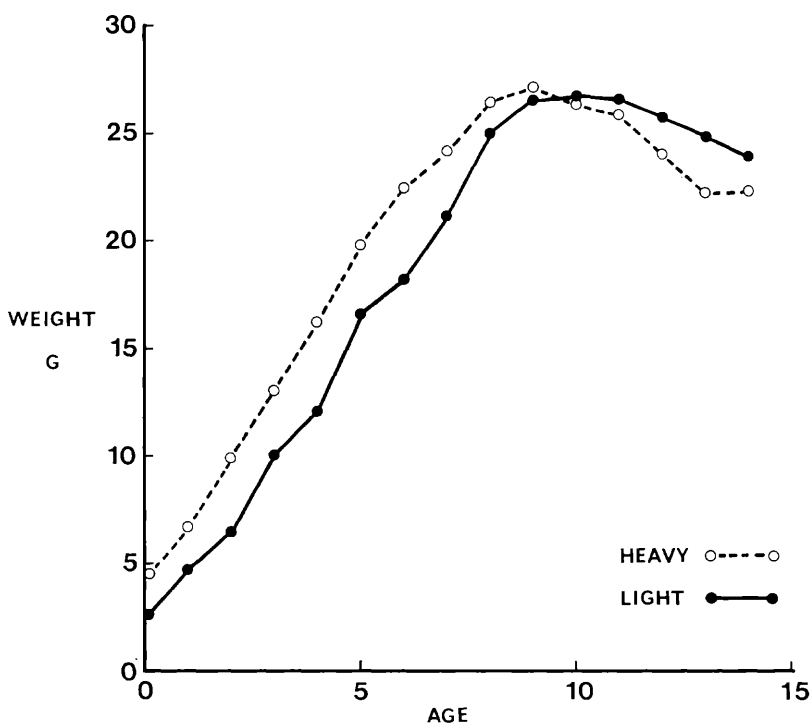
FIGURE 2. Growth curves for House Sparrows of different day 0 weight classes. "Heavy" birds are those of above average day 0 weight, "light" birds those below average.

these birds, and weight differences between chicks of such species cannot be given their conventional interpretation without careful consideration of the position of these weights on the growth curve concerned. Much evidence is now available to show that such weight recession is attributable to changes in the water content of nestlings, particularly in the water content of the integument of these species (Ricklefs, 1968a; Bryant, 1972; O'Connor, 1975a). This accounts for the decline in size of, and eventual reversal of sign in, the correlations with day 0 weight (Fig. 1). Such reversals of sign have not been recorded in previous studies of egg weights in relation to later growth, but it is notable that most studies describe a decline in the strength of the egg weight effect with age (Halbersleben and Mussehl, 1922; Wiley, 1950; Skogland et al., 1952; Schifferli, 1973). At least in the case of the Great Tits (*Parus major*) studied by Schifferli, it is possible to correlate this decline with the onset of weight recession and it would probably be valid to generalize such results by postulating a long-term effect of egg weight upon the subsequent development of the chicks concerned. Both Parsons (1970) and Schifferli (1973) have shown that survival to fledging can be affected by egg weight,

thus demonstrating directly a persistent advantage for larger eggs. Schifferli also showed that this effect was more pronounced in late Great Tit clutches than in early clutches. Because late nesting tits show generally greater within-nest differences than do early nesters (Lack, 1966), this may account for the two-fold reduction in regression slopes apparent between his study and those recorded here for (early) Blue Tits.

A striking feature of the results reported here was the marked difference between the pattern for the House Martin and those for the other two species. In the swallow the size of the chick on the hatching day had no effect upon its subsequent growth, beyond an early but short-lived increase in body weight in heavy chicks. In Blue Tit and House Sparrow, on the other hand, early size differences resulted in significant alteration in timing of subsequent events in the growth process. This difference between the species lends support to an argument advanced elsewhere (O'Connor, 1973 and unpubl. data), that reliance upon an insect aeroplankton liable to unpredictable short-term fluctuation requires that the House Martin nestling possess a highly flexible growth pattern. Such flexibility allows both the duration and the form of nestling weight changes to be adjusted to the levels of food available from day to day. Bryant (1973) has described the diet of nestling martins in detail and has shown that this is closely related in composition to that actually available to the foraging adults. Since Johnson (1969) has shown that insect activity is markedly dependent on weather factors (particularly temperature), day to day variation in food supply with changes in the English weather must constitute for the nestling martin a problem precluding a determinate growth pattern as an optimal growth strategy. Lack and Lack (1951) have presented very similar arguments for growth of the Swift (*Apus apus*) in southern England.

In contrast the food supply of early nesting Blue Tits at Oxford is rather reliable (Gibb, 1950; Lack, 1966) although late nesters do face a declining caterpillar population (Lack et al., 1957; Perrins, 1965). Consequently the growth rate of nestling titmice can be optimized and constrained by selection to a relatively rigid pattern appropriate to food levels anticipated by the female at egg-laying (by her choice of clutch-size) and only secondarily adjustable to the realized levels faced by the young after hatching (Ricklefs, 1968b). Under such circumstances genetically controlled factors such as the size of the egg are likely to have a greater role in shaping the growth curve of individual young, and this is reflected in the acceleration in growth rate shown by the Blue Tits studied here (Table 4). Similarly, the intense sibling competition for a food supply that in general is inadequate for the number of young in the nest (Dawson, 1972; O'Connor, 1973 and unpubl. data) results in House Sparrows in a major role for any initial advantage provided by a larger egg. This is again apparent here, in the advancement of maximum weight and in the shorter nestling period of young which were already large on the day of hatching.

In both Blue Tit and House Sparrow the weight difference between two nestlings with a given weight difference on day 0

increased in the course of the first week. For both species this
differential growth can be attributed to an early increase in the
proportion of body protein devoted to food processing organs,
particularly the alimentary tract and liver (O'Connor in press).
The early development of these organs has also been recorded in
other altricial species (Ricklefs, 1967) and must result in increased
capacity for further growth and development, thus increasing
still further an initial size difference between two young (Table 3).
Although both Blue Tit and House Sparrow showed the effect in
this study there were certain very significant differences of detail
between them. First, the nestlings of both species were distributed
over a number of broods so that the differential growth described
here for differences in day 0 weight (Table 3) could be due to dif-
ferences between siblings or between broods, or to a combination
of both.   In fact results presented elsewhere (O'Connor, 1973)
show that these effects were largely between siblings in the House
Sparrow but between broods in the Blue Tit. Thus although day 0
weights were significantly more variable between broods than
within broods in both House Sparrow ($F = 14.6$, $P < 0.001$)
and Blue Tit ($F = 7.7$, $P < 0.001$) this situation had reversed in
sparrows by the time peak weights were attained ($F = 6.04$,
$0.05 < P < 0.06$).   In Blue Tits peak weights remained more
variable between than within broods ($F = 5.32$, $P < 0.01$). A
second point of difference between the species is that when the
difference in the length of nestling period between the two is
allowed for, differential growth continued for relatively longer
among sparrows than among titmice (Fig. 1). This is a consequence
of greater maturity at hatching coupled with a higher relative
growth rate in the House Sparrow (O'Connor, unpubl. data).
Dawson (1972) has some results that support this because he
showed that egg weight (which contributes to maturity at hatching;
Lack, 1968) and nestling weight on the day after the first
egg hatched in each nest (which weight reflects growth rate) had
statistically independent effects on the length of the nestling period.
Finally, differential growth with respect to day 0 weight began
immediately in House Sparrows, increasing systematically with
age, but only after two days had passed in Blue Tits (Table 3).
This delay is due to brood size increasing over the first two days
for most tit nestlings as further eggs hatch, thus making it harder
for any one chick to monopolize the food supply until it is satisfied.
Indeed, a further consideration is involved here, since newly
hatched titmice are fed relatively sooner after hatching the later
they are in the hatching sequence within any one nest (O'Connor,
1975c). This effect directly opposes the effects of day 0 weight
differences and can be seen as minimizing the possibility of
"runts" developing within the brood. It may also be significant
that in Blue Tits differential growth in consequence of day 0 weight
differences ceased on day 8 (Table 2), the age at which brood size
effects on body weight first became apparent in the species (O'Con-
nor, 1975a). In House Sparrows, on the other hand, brood size
effects are less pronounced (Dawson, 1972; O'Connor, 1973) and

thus not responsible for the pattern of day 0 weight dependence in this species. Hence the superficially very similar effects of day 0 weight in the two species result eventually in very different patterns of growth, respectively reducing (Blue Tit) and increasing (House Sparrow) the possibility of selective starvation of individual chicks within each nest. The incidence of such starvation within a species has been shown to be an adaptive correlate of environmental conditions for breeding (Lack and Lack, 1951; Ricklefs, 1965; O'Connor, unpubl. data).

The results of the present study indicate that there is no single effect of the initial size of a nestling upon its subsequent growth. Instead, differences between individual egg weights or hatching weights are integrated into an overall strategy for growth peculiar to each species in consequence of its particular breeding environment, and assessment of the effects of egg weight or hatching weight is meaningful only when viewed against the background of such a strategy.

SUMMARY

The effects of nestling weight on the day of hatching (day 0) upon the subsequent growth of the nestling are examined in three passerine species. Body weight, wing length, and tarsus length were all well correlated on the day of hatching. Day 0 weight thus served as an index of the overall size of the nestling at that age rather than as a measure of fat reserves. Large day 0 weight led to accelerated growth during the first week of nestling life in Blue Tit and House Sparrow, particularly so in the latter species, but in the aerially feeding House Martin such effects were small and short-lived. In older titmice and sparrows weight recession began earlier the greater their day 0 weights, and in sparrows this led to earlier fledging. In both species wing growth and weight recession increased independently in response to prolongation of the nestling period.

These effects of day 0 weight on the subsequent development of the nestling can be interpreted as components within overall species-specific growth strategies optimizing nestling growth to the environmental milieu of the species.

ACKNOWLEDGMENTS

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