EFFECT OF EPHEMERAL FOOD RESTRICTION ON GROWTH OF HOUSE SPARROWS

CHRISTOPHER A. LEPCZYK[1] AND WILLIAM H. KARASOV

Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706, USA

ABSTRACT.—We tested for the presence of compensatory growth (i.e. faster age-specific growth) following ephemeral periods of food restriction in altricial nestlings using the House Sparrow (*Passer domesticus*) as a model species. To simulate periods of poor food conditions, we raised nestlings in captivity, fed them a synthetic diet, and held them at constant body mass for 48 h beginning on either day 3 or 6 of life. Controls were fed according to an age-specific feeding schedule that yielded normal growth curves. During realimentation, restricted nestlings did not achieve a faster rate of growth than that of controls. Instead, these nestlings either died (all controls lived) or gained mass at a rate similar to that of controls. Consequently, restricted nestlings reached asymptotic mass two days later than control nestlings. Growth of culmen and tarsus was not affected, but growth of the eighth primary was reduced for several days in nestlings restricted at day 6 (i.e. late restricted), although this difference disappeared by the age of fledging. Because surviving nestlings achieved only a 15.9% increase in food consumption compared with unrestricted controls and were unable to translate it into a faster rate of growth, the nestlings may have been growing at a maximum rate. We found no differences between late-restricted and unrestricted nestlings in % water, % protein, % lipid, and % ash. The two groups were of similar maturity as measured by % body water and the water index. Our results are consistent with current theory in that periods of food restriction delayed the schedule of mass accretion by the length of the restriction period. Although House Sparrows have a labile growth rate and developmental time, our results did not support the hypothesis of compensatory growth. Based on this and one other study, compensatory growth does not appear to occur in altricial birds. *Received 6 May 1998, accepted 16 June 1999.*

POSTNATAL GROWTH IN BIRDS is a period of rapid mass gain, tissue maturation, and anatomical development. Given these changes, postnatal growth is viewed as one of the most energetically demanding periods in a bird's life cycle (Ricklefs 1983). Numerous hypotheses have addressed how growth rates are ecologically adapted and potentially constrained (e.g. Lack 1968, Ricklefs 1969, Lilja et al. 1985, Bosque and Bosque 1995). To date, it has been generally accepted that the transition from neonate to fledgling is a relatively fixed process. However, a growing body of literature indicates that growth and development can be quite variable. Sources of this variation include habitat differences (Richner et al. 1989), levels of food abundance (Martin 1987, Cruz and Cruz 1990), diet quality (Boag 1987, Johnston 1993), parasite loads (Møller 1990, Clayton and

Tompkins 1995), weather (Murphy 1985, Keller and Van Noordwijk 1994), and asynchronous hatching (Nisbet et al. 1995). Of these sources, food abundance and diet quality are of particular interest because they represent the energy and nutrients necessary for growth and development.

Different species may respond in markedly different fashions to fluctuations in food abundance or quality. For example, nestling Zebra Finches (*Taeniopygia guttata*) fed a low-quality diet gained mass slower, reached a lower adult mass, and had shorter tarsi than control birds fed a diet that was richer in protein (Boag 1987). Similarly, studies of European Robins (*Erithacus rubecula*) and Carrion Crows (*Corvus corone*) have shown that ephemeral periods of poor food conditions result in abnormal growth, permanent stunting, lower fledging mass, and/or increased mortality (Lees 1949, Richner et al. 1989). In contrast, European Swifts (*Apus apus*; Lack and Lack 1951), Mangrove Swallows (*Iridoprocne albilinea*; Ricklefs 1976), House Martins (*Delichon urbica*; Bryant 1978), and

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[1] Present address: Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824, USA.
E-mail: lepczykc@pilot.msu.edu

White-fronted Bee-eaters (*Merops bullockoides*; Emlen et al. 1991) resumed normal growth rates with no detrimental effects following ephemeral periods of poor food conditions. The ability to adjust growth rate, or the time to reach a developmental endpoint, to prevailing food conditions is termed labile development, which is a form of developmental plasticity (Smith-Gill 1983, Schew and Ricklefs 1998).

Within the context of developmental plasticity lies an interesting but poorly studied phenomenon known as compensatory (i.e. catch-up) growth. Compensatory growth is best defined as an accelerated growth rate relative to age that occurs after a period of poor food conditions or environmental perturbations (Bohman 1955). True compensatory growth is marked by the addition of protein, minerals, and water. This is important to note because growth in its proper sense is represented by increases in protein and skeletal development, not increased fat deposition (Maynard et al. 1979). Originally described in poultry and other agricultural animals (Wilson and Osbourn 1960), compensatory growth has been observed in numerous taxa including invertebrates (Calow and Woolhead 1977), fish (Dobson and Holmes 1984), amphibians (Alford and Harris 1988), and mammals (Wilson and Osbourn 1960). Among birds, compensatory growth has been demonstrated in one precocial species (Japanese Quail [*Coturnix japonica*]; Schew 1995), one semiprecocial species (Jackass Penguin [*Spheniscus demersus*]; Heath and Randall 1985), and one semialtricial species (American Kestrel [*Falco sparverius*]; Negro et al. 1994). Notably scarce are tests of compensation in altricial birds. Konarzewski et al. (1996) tested for compensation in the Song Thrush (*Turdus philomelos*) following a period of food restriction and found no increase in growth rate. However, nestlings were overfed 24 h a day for two days and then sacrificed. Thus, no measure of growth until fledging or adulthood was obtained. The only other study investigating compensatory growth in altricial nestlings found no accelerated growth in European Starlings (*Sturnus vulgaris*; Schew 1995). Nevertheless, given the number of altricial species that exhibit labile development, coupled with the lack of studies, the presence of compensatory growth in altricial birds remains open to question.

Accelerated growth after food restriction in altricial birds would indicate that the normal growth rate is not at the physiological maximum, but rather operates in some optimal manner (Schew and Ricklefs 1998). The question of optimality versus maximality is important because several hypotheses hold that altricial growth rates are maximal, being limited only by some physiological bottleneck. In particular, growth is thought to be limited by bottlenecks in either tissue maturity or the digestive system (e.g. Ricklefs 1969, 1979; Lilja et al. 1985, Konarzewski 1988; Ricklefs et al. 1994). As such, accelerated growth would indicate that nestlings are not growing maximally and hence are not limited by a physiological bottleneck. Another question that can be addressed when investigating accelerated growth is the concept of absolute time schedules. If fledging is a relatively fixed event chronologically, then two possibilities exist following an environmental perturbation: (1) accelerated growth resulting in "normal" fledging mass; or (2) normal or retarded growth resulting in decreased fledging mass. Thus, if compensatory growth or subnormal fledging mass were observed following an ephemeral period of poor food conditions, it would suggest that fledging or asymptotic mass occurs at a relatively fixed time in the nestling's life cycle. Because of the short developmental time in altricial birds, the observation of compensatory growth could significantly alter the view of fixed growth and development.

We used ephemeral food restrictions to simulate environmental perturbations as a means to slow growth and development. Following the restriction, food provisioning became unlimited to allow nestlings an opportunity to respond. Here, we report on the response of nestling House Sparrows (*Passer domesticus*) to these conditions and discuss the implications for altricial birds.

METHODS

Study site.—Natural and artificial nest sites were located in Madison, Wisconsin. Cardboard nest boxes were placed in known House Sparrow breeding sites during January 1995. Beginning in mid-March 1995, all potential nesting locations were visited twice a week to note the onset of laying. From 1 May to 8 August, we strived to visit all nests daily between 1030 and 1330 CST to ensure accurate and consistent aging and structural measurements. At

each visit, we weighed nestlings to the nearest 0.01 g with a portable electronic scale, marked them on their back and scapulars with an indelible marker, and returned them to the nest. Starting on day 3 (hatching = day 0), we measured the length of the culmen, tarsus, and eighth primary (hereafter P8) to the nearest mm.

Experimental design.—To test for compensatory growth following ephemeral periods of food restriction, we set up three laboratory treatments of House Sparrow nestlings: (1) control, (2) early restricted, and (3) late restricted. A fourth group, composed of field nestlings, was set up to monitor nestlings under natural conditions. Subjects for the experimental treatments were removed from their nests between 1030 and 1230 on day 3 and transported to our laboratory at the University of Wisconsin. Only nestlings that had hatched synchronously on day 0 were used in the experiment (i.e. no asynchronous nestlings were used). To control for nest effects, nestlings from the same clutch were randomly assigned to one of the three groups (i.e. all treatments were filled once before adding a second nestling) upon being brought into the laboratory. Nestlings were placed in round (12 × 9 cm) tissue-lined plastic containers and housed in an environmental chamber under constant conditions of 14L:10D photoperiod, 35.6 ± SE of 0.02°C, and 61.9 ± 0.16% relative humidity using a water bath system. Conditions within the chamber were similar to those found in natural nests (Blem 1975). Nestlings in the field group were weighed and measured daily until they left the nest.

Feeding protocol.—All nestlings brought to the laboratory were hand-fed a synthetic liquid diet developed by E. Caviedes-Vidal (pers. comm.) and synthesized by ICN Biomedicals, Inc. The diet was composed primarily of protein (casein), corn starch, and water (see Lepczyk et al. 1998). The diet was 75% water on a wet-mass basis, which provided an adequate amount of water for hydration. Nestlings were removed from the environmental chamber every hour and fed by gavage using a 1-mL syringe for a total of 15 times per day, beginning at 0630. Prior to and following feeding, each nestling's body mass was recorded to account for the mass of food eaten. The volume of food consumed at each feeding was also recorded. Because a pilot study revealed that nestlings fed according to begging did not grow in a similar manner to field nestlings, we adopted an age-specific feeding schedule that previously had yielded normal growth curves (E. Caviedes-Vidal pers. comm.).

The age-specific feeding schedule for control nestlings was 0.3, 0.5, 0.6, 0.75, 0.85, 1.0, 1.25, and 1.5 mL of food per hour for nestlings of ages 3, 4, 5, 6, 7, 8, 9, and 10 to 16 days, respectively. Early restricted nestlings were fed just enough food to keep their body mass constant for 48 h beginning on day 3, whereas late-restricted nestlings were fed in a like manner as control nestlings until day 6, at which

time they were placed on a similar mass-maintenance diet for 48 h. The mass-maintenance level was found to be 0.2 mL food per hour for early restricted nestlings and 0.4 mL food per hour for late-restricted nestlings based on the pilot group of nestlings. After 48 h of maintenance rationing, early restricted and late-restricted nestlings were fed to satiation every hour using a six-step feeding hierarchy. First, we tried feeding >125% of the age-specific level for control nestlings of the same chronological age. If the nestling would not consume >125%, we then tried feeding 125% of the age-specific level for control nestlings of the same chronological age. As a third step, we fed at an hourly rate that provided the same total amount of food during the nestling period as control nestlings received. This rate was determined to be either 0.06 mL per hour for early restricted nestlings.or 0.11 mL per hour for late-restricted nestlings above the age-specific control level. The fourth step was feeding the restricted nestlings at the age-specific control rate. If a nestling would not accept the control level, then it was fed whatever it was willing to accept. Finally, if the nestling refused to eat, was satiated, or regurgitated, it was skipped for that hour. To ensure that all nestlings reached fledging mass, they were fed through day 16 (average fledging age is 14 to 15 days; Weaver 1942, Summers-Smith 1967). On the morning of day 17, nestlings were moved to individual 45 × 32 × 60 cm metal cages. Nestlings were transitioned to the powdered form of the diet and provided with food and water *ad libitum.* We measured fledglings daily through day 30 and then weekly through day 55.

Analysis of growth curves.—Growth data for surviving nestlings of each group were fit using the integrated Richards equation as described by Brisbin et al. (1986) and modified by Leberg et al. (1989):

$$M_t = [A^{(1-m)} - [A^{(1-m)} - M_0^{(1-m)}] \cdot e^{(-2t/T) \cdot (1+m)}]^{1/(1-m)}$$
$$+ e_i, \tag{1}$$

where M_t is body mass at time t, A is asymptotic mass, m is the Richards shape parameter, M_0 is mass at hatching, and T is the growth period (i.e. the approximate time to reach asymptote; Richards 1959). Because both laboratory groups displayed continued growth beyond an asymptote (as a result of the feeding protocol), the fitting procedure was modified as follows. Control individuals were constrained by a 25-g asymptote (the mean A of field nestlings) with all data points above 25 g being excluded from the curve-fitting procedure. Late-restricted nestlings were constrained in the same manner as control nestlings and were further modified by removing the two days at which body mass was held constant (i.e. data were shifted back two days by recoding day 8 as day 6, etc.). Parameter estimates for m were 2.28 ± 0.47 and 1.75 ± 0.27 for the control and late-restricted nestlings, respectively (see Results for estimates of

T). Early restricted nestlings were not fit to the model because none survived until fledging (see Results).

Carcass analysis.—Because true compensatory growth is defined as the addition of lean body mass, we performed body composition analyses of control and late-restricted nestlings on day 11 (early restricted nestlings excluded because most did not survive for 72 h after restriction). We chose day 11 to allow nestlings in the late-restricted group several days of *ad libitum* feeding. Nestlings were sacrificed between 1230 and 1630, at which time they were dissected to remove the stomach, liver, and intestines for biochemical measures (Lepczyk et al. 1998). The stomach was emptied, blotted, and weighed, whereas the liver was simply blotted and weighed. The entire carcass (minus the intestines) of each individual was then freeze-dried to constant mass and homogenized. Two separate 0.75-g samples of the dry homogenate were extracted for crude lipids in a Soxhlet apparatus using petroleum ether (Helrich 1990). The samples were redried and the lipid content calculated. Protein content was determined by the macro Kjeldahl method (Helrich 1990) using replicate 0.5-g samples of the dry homogenate. Ash content was determined as the mass remaining after burning replicate 0.50-g samples in a muffle furnace at 525°C. Percentages of each component with respect to wet mass were calculated as [100 × mass of component] / wet body mass. Total water and lipid masses were divided by lean dry mass to calculate water and lipid indices, respectively (Blem 1975).

Data analysis.—The times taken to reach near asymptote (i.e. T) were analyzed with the covariates of mass on day 0 (M_0) and day 3 (M_3) and the categorical variable of group (G). Body mass covariates were initially chosen because each nestling had slightly different hatching masses (day 0) and slightly different handling effects (day 3). All possible model combinations were investigated using Mallows C_p statistic (Draper and Smith 1981) to find the most parsimonious model explaining T. The T of surviving nestlings was best estimated by the model:

$$T_i = \alpha_0 + \alpha_1 G + e_i, \qquad (2)$$

where $T_i = T$, α_0 is a constant, α_1 is a coefficient, and e = error. Daily rate of change in body mass (i.e. incremental growth) was analyzed for each 24-h increment using ANCOVA, with initial body mass for the period as the covariate. Structural growth was analyzed with repeated-measures ANOVA and compared using the Wilks' lambda statistic. Length of P8 was analyzed for each 24-h increment in the same fashion as incremental body mass. The multivariate general linear hypothesis module in SYSTAT was used for data analysis (Wilkinson 1992). Group differences other than structural measurements were compared using Tukey's HSD procedure (Zar 1996). Body compositions and food consumption were analyzed using a two-tailed *t*-test. Means are reported ± 1 SE unless otherwise noted.

RESULTS

The proportion of nestlings that survived from hatching to day 16 or fledging was 0.914 (32 of 35), 1.0 (9 of 9), 0 (0 of 9), and 0.6 (6 of 10) for field, control, early restricted, and late restricted, respectively. All nestlings survived the 48-h food restriction, but mortality began occurring within 48 h after restriction in both early and late-restricted groups. A single early restricted nestling survived until day 15 but subsequently died.

Mean food consumption before restriction was 24.3 ± 0.3 g and 24.4 ± 0.5 g for control and late-restricted nestlings, respectively ($t = -0.17$, df = 13, $P = 0.87$). During the 48-h restriction, mean food consumption was 25.6 ± 0.2 g and 12.1 ± 0.03 g for control and late-restricted nestlings ($t = 60.74$, df = 13, $P < 0.0005$). Following restriction, late-restricted nestlings consumed more food than did control nestlings ($t = -6.93$, df = 13, $P < 0.0005$). Mean food consumption following restriction was 185.6 ± 0.2 g for control nestlings and 215.2 ± 5.3 g for late-restricted nestlings. Although late-restricted nestlings consumed more food after restriction, it was difficult to overfeed them as indicated by the increase in consumption of only 15.9%. Furthermore, nestlings regurgitated when fed more than the 15.9%.

Due to small sample size of field nestlings after day 11, structural analyses were performed from days 3 to 11 for comparison among all three groups. Tarsus length (Fig. 1) and culmen length (Fig. 2) did not differ among field, control, and late-restricted nestlings (repeated-measures ANOVA; tarsus, $F = 0.728$, df = 16 and 70, $P = 0.757$; culmen, $F = 0.613$, df = 16 and 70, $P = 0.281$). However, development of P8 (Fig. 3) was different among treatments ($F = 0.414$, df = 14 and 72, $P = 0.002$) owing to several days of different incremental growth in one of the treatments. Final structural lengths of the laboratory-raised nestlings were analyzed using a repeated-measures ANOVA from days 3 to 55. Notably, one late-restricted nestling died, and four nestlings had broken shafts on P8 before day 55, which reduced sample sizes to 9 and 5, 9 and 5, and 7 and 3 in control and late-restricted nestlings for tarsus, culmen,
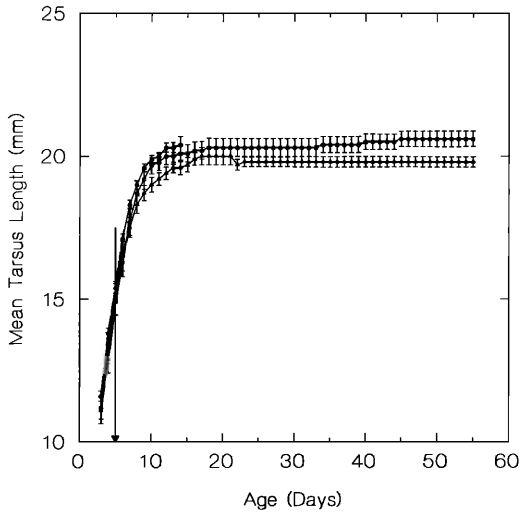
FIG. 1. Tarsus length ($\bar{x} \pm$ SE) as a function of age for field (filled circles), control (open circles), and late-restricted (triangles) nestlings. Arrow denotes onset of 48-h food restriction.
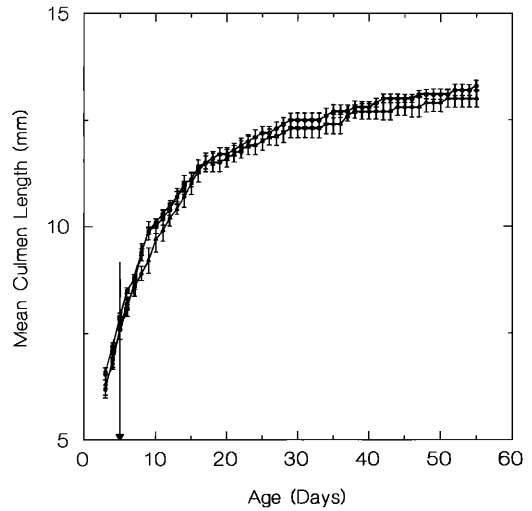

FIG. 2. Culmen length ($\bar{x} \pm$ SE) as a function of age for field (filled circles), control (open circles), and late-restricted (triangles) nestlings. Arrow denotes onset of 48-h food restriction.

and P8, respectively. No significant differences occurred between control and late-restricted nestlings in final lengths of the tarsus ($F = 2.17$, df = 1 and 12, $P = 0.17$; Fig. 1), culmen ($F = 0.61$, df = 1 and 12, $P = 0.45$; Fig. 2), and P8 ($F = 2.51$, df = 1 and 8, $P = 0.15$; Fig. 3).

Control nestlings reached T faster than late-restricted nestlings ($F = 8.66$, df = 1 and 13, $P = 0.011$; Fig. 4). Mean T-values were 13.8 $\pm$ 0.4 days for control nestlings and 15.5 $\pm$ 0.5 days for late-restricted nestlings. Although the control nestlings maintained a slightly higher body mass than the late-restricted nestlings, the difference was not significant after day 13 ($t = 2.09$, df = 13, $P = 0.057$; Fig. 5A). Over the course of their development, daily rates of change in body mass varied among field, control, and late-restricted nestlings (Fig. 5B). The telltale sign of compensatory growth would have been a significantly faster rate of gain in the late-restricted group than the control group during the days following the end of food restriction. Although this was not observed based on ANCOVA for the three groups (Fig. 5B), t-tests comparing the two laboratory groups alone indicated a significantly higher mass gain on the first day following restriction ($t = -5.11$, df = 13, $P = 0.0002$) and a significantly lower mass gain on the second day ($t = 3.93$, df = 13, $P = 0.0017$). In the two days following restric-

tion, mass gain of late-restricted birds did not differ significantly from that of controls by either ANCOVA ($F = 0.027$, df = 1 and 12, $P = 0.87$) or a t-test ($t = -1.48$, df = 13, $P = 0.16$). A power analysis of the data over two days (two-sample t-test with $\alpha = 0.05$ and $\beta = 0.2$) indicated that a difference in mass gain between the two groups of at least 1.7 g would
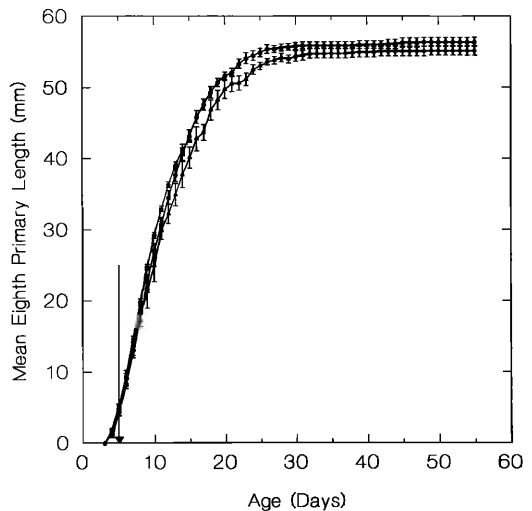

FIG. 3. Length of P8 ($\bar{x} \pm$ SE) as a function of age for field (filled circles), control (open circles), and late-restricted (triangles) nestlings. Arrow denotes onset of 48-h food restriction.
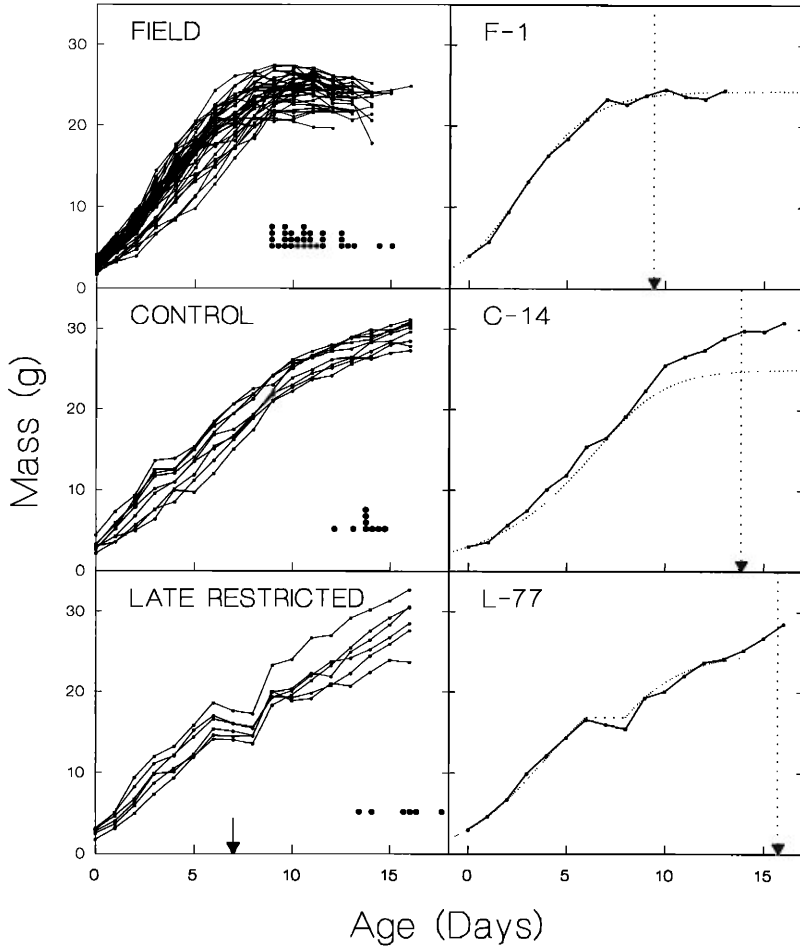
FIG. 4. Daily mass of individuals and fitted growth curves. The left column shows daily mass for individuals of each group with histograms representing the time to reach T in the Richards growth model (equation 1). The arrow in the late-restricted group denotes initiation of 48-h food restriction. The right column illustrates fitted growth curves for a single individual within each respective group. Dashed lines represent the fit to equation 1, and the dashed arrow represents the time to reach T in equation 1.

have been required for us to detect it. Besides these differences, the only other time that late-restricted nestlings gained mass faster than control nestlings (field nestlings not included) was when growth tailed off in the controls on days 14 to 15 ($t = -3.24$, df = 13, $P = 0.006$).

Body composition analysis in control and late-restricted nestlings revealed no significant differences in the content of lipid ($t = 0.33$, df = 14, $P = 0.75$), protein ($t = -0.67$, df = 14, $P = 0.51$), ash ($t = -0.90$, df = 14, $P = 0.38$), and water ($t = 0.59$, df = 14, $P = 0.57$; Table 1). Similarly, no significant differences occurred between the groups in water ($t = 0.78$, df = 14, P

$= 0.45$) and lipid ($t = 0.78$, df = 14, $P = 0.45$) indices (Table 1).

DISCUSSION

Growth following realimentation.—Following 48 h of food restriction, late-restricted nestlings gained mass at a similar rate to control nestlings, despite being offered excess food and consuming 15.9% more than control nestlings. The late-restricted nestlings reached T roughly two days later than control nestlings, corresponding to their two days of food restriction (Fig. 4). This delayed maturation is consistent
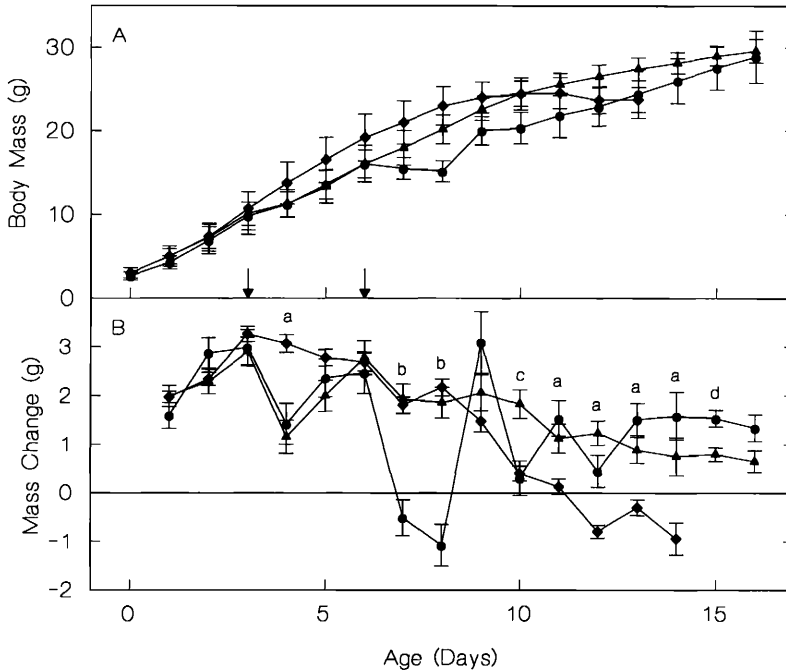
FIG. 5. Mean daily mass and incremental growth of House Sparrow nestlings. (A) Mean daily mass (±SE) of field (filled circles), control (open circles), and late-restricted (triangles) nestlings, respectively. The left arrow denotes the time when control and late-restricted nestlings were brought into the laboratory, and the right arrow denotes onset of the 48-h food restriction. (B) Daily rates of change in body mass using least square means (±SE) for each treatment. Letters denote significant differences between groups on a given day according to a Tukey HSD multiple comparisons test. Field differed from control and late restricted (a), late restricted differed from field and control (b), control differed from late restricted (c), and control differed from late restricted when field was absent (d).

with the prevailing hypothesis that an environmental perturbation delays maturity (e.g. asymptotic mass or fledging) by a length of time equal to the perturbation (Schew and Ricklefs 1998). Furthermore, the inability of nestling House Sparrows to achieve compensatory growth following an ephemeral food restriction is consistent with European Starlings

TABLE 1. Body composition analysis for 16 House Sparrow nestlings (8 per treatment) at 11 days of age. Values are treatment means ± SD.

Component	Control nestlings	Late-restricted nestlings
% Lipid	7.02 ± 0.72	6.86 ± 1.10
% Protein	14.90 ± 0.45	15.22 ± 1.27
% Ash	2.30 ± 0.11	2.41 ± 0.32
% Water	71.71 ± 1.01	71.20 ± 2.26
% Lean dry mass	21.27 ± 0.68	21.94 ± 1.71
Water index	3.38 ± 0.15	3.27 ± 0.35
Lipid index	0.33 ± 0.04	0.31 ± 0.05

(Schew 1995), which also lack the ability to accelerate their growth rate.

Although a period of accelerated mass gain appeared within 24 h of realimentation (Fig. 5B), it can be attributed to a gut-fill phenomenon (see Wilson and Osbourn 1960) that occurred within the first 3 to 4 h after restriction, when nestlings were begging but literally could not consume any more food without regurgitating. The phenomenon disappeared the following day, during which mass gain in the previously restricted birds was somewhat lower than the controls. Hence, over the two-day period following restriction, and for subsequent days, the incremental growth did not differ significantly between control and late-restricted nestlings except for days 14 to 15, when the growth of the former group was tailing off (Fig. 5B). The control and late-restricted nestlings continued to add mass well after the field nestlings had reached asymptotic mass, and

they were heavier than the field nestlings. This added mass was partially due to an increase in subcutaneous fat, which was visible in the pectoralis region on days 15 and 16. The fat decreased noticeably, and body mass declined to a lower asymptotic level, after the birds' transition to cages.

Growth of the culmen and tarsus in late-restricted nestlings was not noticeably affected by the restriction (Figs. 1 and 2) and subsequent realimentation. Growth of P8 (Fig. 3), on the other hand, differed among field, control, and late-restricted nestlings. When viewed incrementally, feather growth did not show any consistent group trend. Notably, late-restricted nestlings had slower feather growth on two occasions immediately following realimentation. Similar reductions in rates of feather growth have been observed in European Swifts (Lack and Lack 1951) and Mangrove Swallows (Ricklefs 1976) following periods of poor food conditions. Thus, of the structural components measured, only P8 showed any negative response to food restriction. Overall, though, the final length of P8 did not differ among treatments (Fig. 3).

Results of our body composition analysis between control and late-restricted nestlings were similar to those of Blem (1975) and Myrcha et al. (1973). Percent body water and the water index were used as indices of tissue maturation (Ricklefs and Webb 1985, Konarzewski 1988), and hence age, to compare control and late-restricted nestlings. Lack of a difference between the two groups in these indices indicated that they were of the same physiological and chronological age. Furthermore, the lack of disparity in physiological age indicated that physiological and chronological age did not become decoupled during restriction in the late-restricted nestlings. Because no differences occurred between control and late-restricted nestlings in body fat, protein, or ash, we surmise that the late-restricted nestlings had added tissue in a manner similar to that of control nestlings. Moreover, the lack of differences indicates that true growth between the two treatments was similar as of day 11 and was not an artifact of fattening.

Feeding protocol and survival.—The inability of altricial nestlings to feed themselves presented a potential challenge in studying growth and development of House Sparrows. Because begging was not a reliable indicator of satiation, we used a previously developed feeding protocol that yielded growth and development similar to wild nestlings (E. Caviedes-Vidal pers. comm.). Similarly, begging was not reliable in the post-restriction period of early and late-restricted nestlings. As such, we developed a hierarchical feeding protocol that offered food *ad libitum* without overfeeding. Although late-restricted nestlings consumed significantly more food than control nestlings, they were not able to translate this into a faster growth rate. The explanation for this lack of increased growth rate is that the food had a shorter residence time (mean retention time), which reduced digestive efficiency and hence resulted in a rate of energy gain similar to that of control nestlings (Lepczyk et al. 1998). Furthermore, our methodology only varied the quantity of food delivered and not the quality, which might be a factor during realimentation.

The pattern of survival differed markedly among groups. Although field nestlings showed high fledging success compared with reported rates (Weaver 1942, Seel 1970), it should be kept in mind that only synchronously hatched nestlings from surviving clutches were included. The lack of mortality in control nestlings indicates that the diet, feeding protocol, and environmental chamber provided adequate energy, nutrients, and conditions for raising nestling House Sparrows. However, a handling effect was detected in the form of lower growth rates on day 3 when the nestlings were first transferred to the laboratory (Fig. 5). Cause(s) of mortality in the early and late-restricted nestlings are unknown. In a similar study of European Starlings, nearly all nestlings that experienced 72 h of mass-maintenance feeding on days 3 or 8 survived until fledging (Schew 1995). Notably, however, the nestling starlings were returned to their original nests to be raised by their parents following the restriction. Because of our interest in investigating digestive physiology during and following food restriction, as well as the potential for nest abandonment, returning nestlings to their nests was not a feasible option. Thus, within the laboratory setting, our results are consistent with the conclusion of Wilson and Osbourn (1970) that "undernutrition in the earlier stages of growth is more detrimental to an animal than restriction at a later stage." Be-

cause the duration and severity of the restriction were similar for early and late-restricted nestlings, yet the response was markedly different, perhaps the early restricted nestlings were more susceptible to food restriction than were the late-restricted nestlings. However, the control and late-restricted nestlings experienced a minor food restriction on day 3, as evidenced by the handling effect (Fig. 5), but did not display a similar mortality rate as the early restricted nestlings. Another possibility is that food restriction may have put nestlings into a state of chronic malnutrition that lasted beyond the restriction period. Finally, it is also important to note that the actual level of food restriction might be crucial for later development and survival. However, as previously mentioned, nearly all European Starlings nestlings held at constant body mass for 72 h survived until fledging (Schew 1995), suggesting that a mass-maintenance feeding level is not detrimental to post-restriction survival in and of itself.

Compensatory growth and labile development in altricial birds.—Thus far, the presence of compensatory growth in altricial nestlings has not been demonstrated. Indeed, Schew and Ricklefs (1998) suggest that whether compensatory growth occurs in any birds remains open to question owing to the way in which growth data are typically expressed. The fact remains, however, that some altricial birds display labile growth rates and development times, such as White-fronted Bee-eaters (Emlen et al. 1991), European Swifts (Lack and Lack 1951), Mangrove Swallows (Ricklefs 1976), and House Martins (Bryant 1978). Although the House Sparrow has not previously been described as a labile developer, older nestlings showed several signs of lability. First, late-restricted nestlings reached a similar fledging mass as control nestlings. Second, no abnormal growth or stunted structural development occurred. Thus, the House Sparrow represents a species that, to some extent, displays a labile growth rate resulting in a longer nestling period when faced with poor food conditions. Such lability helps to explain the wide range in fledging times for House Sparrows reported in the literature (12 to 18 days; Weaver 1942, North 1973).

The presence of labile development without accelerated growth suggests that altricial nestlings reduce growth and development in the face of poor food conditions, and that under good food conditions, they grow at a maximal rate. In altricial nestlings, this maximal growth rate may be the optimal growth rate. Notably, although the optimal growth rate has been proposed in terms of external selection pressures, such as risk of predation (Lack 1968, Bosque and Bosque 1995), and physiological constraints (Ricklefs 1969, 1979), both views consider altricial nestlings to be growing maximally (i.e. optimal growth rate can be the maximum growth rate). On the other hand, growth rates in poultry and wild precocial birds do not appear to be maximal growth rates as indicated by food restriction and realimentation experiments that demonstrate accelerated growth. In poultry, for example, accelerated growth is associated with increased feeding rates (Auckland et al. 1969) or increased "feed efficiency" (Moran 1981, Plavnik and Hurwitz 1988, Santoso et al. 1995). Because these increases do not occur in control individuals of the same chronologic age, birds that experience *ad libitum* conditions may be growing at sub-maximal rates. One caveat of these studies is that poultry are under intense artificial selection for specific characteristics (e.g. faster growth and feed conversion), which complicates comparisons with wild birds. However, given that wild precocial birds grow at sub-maximal rates, the comparison has validity. Thus, precocial and domestic birds appear to grow at sub-maximal rates, whereas altricial birds appear to be growing maximally.

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