ASYNCHRONOUS HATCHING AND FOOD LIMITATION: A TEST OF LACK'S HYPOTHESIS

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ABSTRACT.—Lack's (1954, 1968) hypothesis that asynchronous hatching of altricial birds is an adaptive response to unpredictable food shortages during the breeding season was examined in the highly granivorous Zebra Finch (*Poephila guttata*). I compared growth and survival of nestlings in asynchronous and artificially created synchronous broods reared under food-limited and food-abundant conditions in an aviary. I also examined the role of parental experience on survival and growth of nestlings.

There was no differential mortality of Zebra Finch nestlings due to either asynchrony or food abundance. Young in abundant food treatments grew more rapidly, however, than those in food-restricted treatments. Heaviest Zebra Finch nestlings in a brood grew more quickly than their lightest siblings when food was limited, supporting Lack's hypothesis. Further, differential survival of light and heavy siblings occurred when food was abundant, suggesting that asynchronous hatching can be maladaptive under some ecological conditions. Nestlings reared by inexperienced parents suffered greater mortality and slower growth when food was abundant than nestlings raised by experienced parents. Prefledging mass was correlated with size at adulthood. *Received 25 November 1987, accepted 17 September 1987.*

LACK (1954, 1968) proposed that asynchronous hatching in altricial birds is an adaptive response to potential unpredictable food shortages. According to this hypothesis, a disparity in the size of young at the completion of hatching results in a hierarchy among siblings, and the youngest sibling receives less food. Brood reduction by starvation of the youngest chick may occur during times of food scarcity, and result in a higher probability of survival for the remainder of the brood than if all young were fed equally (Ricklefs 1965). Few studies have tested Lack's hypothesis experimentally while documenting or manipulating food abundance (e.g. Slagsvold 1982, 1985; Bengtsson and Ryden 1983; Fujioka 1985; Mock and Ploger 1987). In this study I examined the effect of hatching asynchrony on nestling Zebra Finches (*Poephila guttata*) reared in captivity under conditions of food limitation and food abundance. I simulated synchrony in broods by manipulating eggs before incubation and was thus able to compare survival and growth of "synchronous" broods with "asynchronous" broods.

I examined three predictions derived from the hypothesis that when food is scarce, asynchronous hatching facilitates differential growth and mortality of young, providing growth or survival benefits to older siblings. First, when food is limited, late-hatched nestlings of asynchronous broods are more likely to die or grow more slowly than their older siblings than are last-hatched nestlings of synchronous broods. Second, heaviest nestlings of asynchronous broods grow faster than those of synchronous broods when food is limiting. Furthermore, one would expect that asynchronous hatching is not disadvantageous when food is abundant. Third, there are no differences in growth and survival of nestlings by rank in the brood hierarchy in asynchronous or in synchronous broods when food is abundant. I also estimated how parental experience influences survival and growth of nestlings and the relationship between growth rates, prefledging mass, and size at adulthood.

METHODS

Study animals.—Zebra Finches range widely throughout Australia in arid, semiarid, and humid zones. They breed in large colonies during the rainy season and are almost exclusively granivorous throughout the year; grass seeds constitute more than 98% of their diet during the breeding and nonbreeding seasons (Zann and Straw 1984). Zebra Finches feed their normally asynchronously hatched young partially digested seeds by regurgitation. Nestlings temporarily store seed in esophageal diverticula, a feature common in species that feed primarily seeds

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to their young during the nestling period. Nestlings leave the nest at 13–16 days of age.

During 1984 and 1985, 22 pairs of adult Zebra Finches were housed separately in 164 × 164 × 82 cm cages provided with covered, wicker nest baskets. Breeding birds were housed in 3 rooms under controlled temperature (22–25°C), humidity (50%), and day length (14 h). Young birds were moved to a free-flight room 2 weeks postfledging or when bills began to turn orange (a sign of sexual maturity).

Birds were maintained on a diet of Kellogg Finch Mixture, crushed Science Diet cat food, and fresh spinach provided *ad libitum*. Vitamins and minerals were diluted in drinking water; crushed oyster-shell grit and cuttlebones were also provided. To establish appropriate food levels for limited and abundant food treatments, daily seed consumption was measured for 12 pairs during incubation and while rearing 10 broods of 1–4 young to 14 days of age. During the food-consumption trials birds were fed preweighed seed that was collected 24 h later; hulls and fecal matter were then removed and the seed reweighed. I assumed that the seed required per day to maintain 2 adult birds was equal to the average mass of seed consumed daily by 2 parents during incubation (6.27 g). This figure is consistent with daily energy requirements determined by Vleck (1981). Additional seed consumed during brood rearing was assumed to reflect daily food requirements for growth and maintenance of young at various ages (Table 1). Food (seed, crushed catfood [0.5 g/day], and spinach) was provided 2–3 times daily to parents and young of food-limited treatments. The amount of food provided to the treatment groups approximated $(n - 1)DR + (0.6)DR$, where n = brood size and DR = daily food requirement (g) for one nestling. Food-limitation treatments were begun within one day of the completion of hatching and ended on brood day 14 (the day the first nestling hatched was considered brood day 0 for that brood). Food was provided *ad libitum* to birds in food-abundant treatments.

Synchrony manipulations.—Thirty-six broods were assigned to one of four treatments of a 2^2 factorial design, with independent variables of food abundance (limited or abundant) and degree of hatching synchrony (synchronous or asynchronous; see Table 2). Eggs from nests assigned to synchronous treatments were removed from nests at laying, weighed, measured, and stored in protective containers at 18–20°C. Abnormal development of embryos is unlikely to occur below physiological zero temperature (25–27°C; Drent 1973). Eggs were reweighed and returned to the nests at the completion of laying, so that incubation began on all eggs simultaneously. There was no evidence of reduced hatching success of stored eggs; eggs lost on average only 0.01 g during storage.

Broods in which the difference in nestling mass (DNM = mass of first-hatched nestling − mass of last-hatched nestling within 1 day of the completion of hatching) was less than 0.5 g were classified as synchronous, and broods in which DNM exceeded 0.5 g were considered asynchronous. Seven of 24 unmanipulated (asynchronous) clutches hatched synchronously and were reassigned to the appropriate category.

TABLE 1. Daily mean seed requirements of nestlings aged 1–14 days, as determined from seed-consumption trials.

Age (days)	Seed/nestling (g)
1	0.00
2	0.10
3	0.31
4	0.53
5	0.74
6	0.96
7	1.18
8	1.34
9	1.61
10	1.83
11	2.05
12	2.27
13	2.47
14	2.70

Nestlings were weighed (0.001 g, Sartorius balance), measured (wing chord and tarsus, ±0.01 mm, dial vernier calipers), and individually marked with nail polish on hind toenails at 1–2 day intervals until 14 days of age, at age 20–24 days, and after adult plumage and bill coloration developed. The amount of food stored in the esophageal diverticulum was assessed visually at each weighing and ranked from 0 (none) to 4 (full). The presence of dark circular palate markings, thought to be important in parental feeding, was also noted for each nestling. Parents were weighed 1–2 days after the first young hatched and again at brood day 14. Food was removed from cages 1 h before parents were weighed so that the esophagi were empty of seed.

Data analyses.—I used stepwise logistic regression analysis (Engelman 1979) to identify factors correlated with nestling survivorship. Variables examined included: (1) food abundance (limited or abundant), (2) parental experience (no previous successful nesting attempts or successful rearing of at least one offspring before the current nesting attempt), (3) degree of synchrony (synchronous or asynchronous), (4) brood size (range 2–6 chicks) during at least 70% of the nestling's growth period, (5) rank of nestling in a size hierarchy (lightest, heaviest, or intermediate in mass at the time of completion of hatching or, if siblings died, during 70% of its growth period), and (6) presence of palate markings (absent or present). In the logistic regression analysis, only variables with a P-value less than 0.10 were entered into the model.

I used the relative mass of nestlings as an indicator

TABLE 2. Data used in survivorship and growth analyses.

Variable	Limited food		Abundant food		Total
	Syn	Asy	Syn	Asy	
No. of young	35	28	20	49	132
No. of broods	10	8	6	12	36
Percentage of nestlings reared by experienced parents	80.0	89.3	95.0	87.8	87.1
Percentage male (n = 106)	54.2	29.6	18.8	43.6	38.7
Percentage with palate markings	77.1	82.1	70.0	87.8	81.1
Mean brood size (SD)	3.5 (1.08)	3.5 (1.07)	3.0 (1.27)	3.8 (1.12)	3.5 (1.11)
Percentage survival	82.9	96.4	80.0	85.7	

of relative nestling age because precise hatching times were unavailable (see Slagsvold 1986, Skagen 1987). I believe this method is reliable because nestlings weighed 0.6–0.9 g at hatching and gained on average 0.6 g/day. First- and last-hatched nestlings are easily distinguished from each other and generally from intermediates by relative size. Because not all young reached asymptotic mass by age 14 days, I did not use growth curves that required specification of asymptotic mass to described growth. Rather, growth curves from 0 to 14 days of age were fitted to a polynomial (cubic) equation, and mass at days 7 and 12 was estimated from the resulting equation. I estimated the growth rate (daily growth increment) using linear regression analysis. The slope of the line of best fit between 1 and 10 days of age was used as an estimate of the overall growth rate.

Multiple analyses of variance were used to determine the main effects and interactions of food abundance (limited coded as 0, abundant as 1), the degree of synchrony (synchronous coded as 0, asynchronous as 1), and nestling rank in brood hierarchy (lightest individual coded as 1, heaviest as 3, intermediates as 2) on growth parameters of young surviving the nestling period. Brood size (small [2–4 chicks] coded as 1, large [5–6] as 2), parental experience (inexperienced coded as 0, experienced as 1), sex of young (male coded as 1, female as 2), and presence of palate markings (no markings coded as 0, markings present as 1) were specified as covariates.

Statistical procedures were performed by Minitab (Ryan et al. 1976), SPSSX (Nie et al. 1975, SPSS Inc. 1983), and BMDP (Dixon and Brown 1979). Variation around the mean is reported as $\bar{x} \pm$ SD unless otherwise specified. Results were considered significant at the 0.05 level.

RESULTS

The normal hatching pattern of Zebra Finch eggs was asynchronous, and unmanipulated clutches hatched on average over a 2-day period. In 16 synchronous broods DNM averaged 0.23 g (SE = 0.033), and DNM of 20 asynchronous broods averaged 1.07 g (SE = 0.114).

Of 150 nestlings hatched by 20 adult pairs, 31 (20.7%) died before fledging. Nestling mortality occurred at an average age of 3.4 days (±2.81, range 0–9, median 3). Four broods (totaling 13 nestlings) in which all nestlings died were omitted from subsequent data analyses because the deaths were attributed to causes unrelated to the experimental treatments (e.g. nestlings fell or were thrown out of nests). I also eliminated from the data set 5 broods that had only one nestling because hatching synchrony was not applicable to these broods. The resulting data used in further analyses are presented in Table 2. The response variables (growth rates, nestling mass at ages 7 and 12 days, and adult mass) were normally distributed about their means (Knight 1986).

TABLE 3. Mean (±1 SD) growth rates, mass of nestlings at 7 and 12 days of age, and adult mass of nestlings reared under conditions of food limitation and abundance.

Variable	Overall (n = 114)	Limited food (n = 56)	Abundant food (n = 58)	Tests of significance of difference	
				t	P
Growth rate (g/day)	0.601 ± 0.193	0.541 ± 0.183	0.659 ± 0.187	3.40	0.0009
Mass (g) at 7 days	4.31 ± 1.20	4.03 ± 1.11	4.59 ± 1.23	2.57	0.011
Mass (g) at 12 days	7.42 ± 1.75	6.86 ± 1.84	7.96 ± 1.48	3.52	0.0006
Adult mass (g)	12.15 ± 1.19	12.06 ± 1.11	12.24 ± 1.28	0.77	0.44

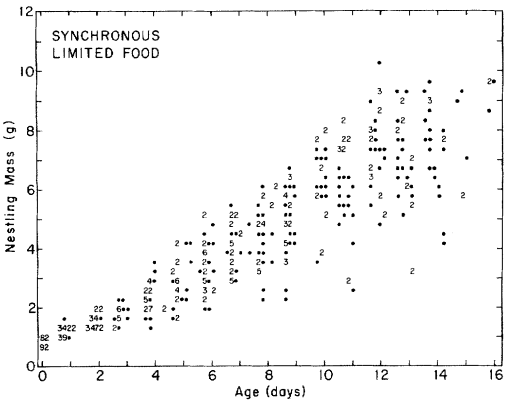

Fig. 1. Daily mass of 29 nestling Zebra Finches in 10 synchronous broods reared under food-limited conditions. Dots represent single data points; numbers 2–9 represent overlapping data points.

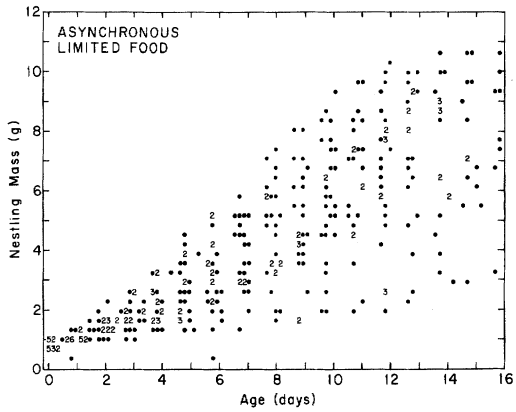

Fig. 3. Daily mass of 27 nestling Zebra Finches in 8 asynchronous broods reared under food-limited conditions. Dots represent single data points; numbers represent overlapping data points.

Effects of food abundance on nestling growth and survival.—Survivorship patterns of 132 nestlings in 36 broods (Table 2) were examined to determine the importance of 7 variables on nestling survival. Food abundance had no significant effect on overall survivorship, nor did it enter the logistic regression model. Young died as often when food was abundant (10 of 69 nestlings) as when food was limited (7 of 63 nestlings). There was also no difference (t_{16} = 1.70, $P > 0.10$) in age at mortality between nestlings in food-limited (4.9 ± 3.08 days) and food-abundant treatments (2.6 ± 2.34 days).

Food abundance influenced significantly the growth of nestlings. Nestlings grew faster and attained greater mass at 7 and 12 days of age when food was abundant than when food was restricted (Table 3). These differences were not due to differences between treatments in experience of parents (t_{113} = 0.26, $P > 0.50$), brood size (t_{113} = 0.28, $P > 0.50$), sex ratios (χ^2 = 0.51, df = 1, $P > 0.25$), nor presence of palate markings (χ^2 = 0.73, df = 1, $P > 0.25$). In addition, there was more divergence through time of mass of nestlings reared under food-limited than food-abundant conditions; this pattern was most pronounced in asynchronous broods (Figs. 1–4).

Hatching asynchrony and nestling rank in the brood

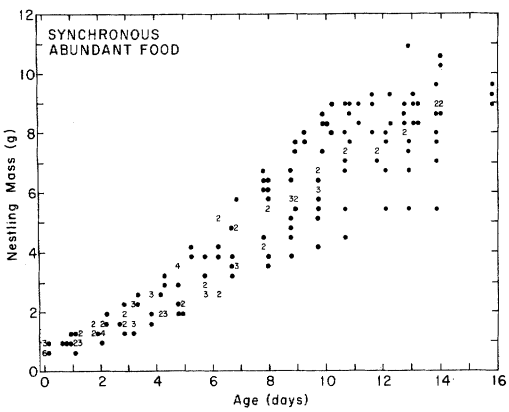

Fig. 2. Daily mass of 16 nestling Zebra Finches in 6 synchronous broods reared under food-abundant conditions. Dots represent single data points; numbers represent overlapping data points.

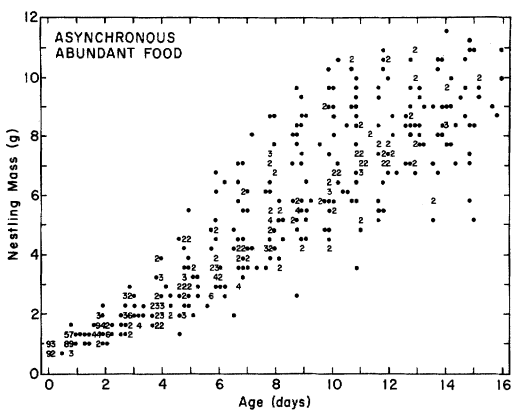

Fig. 4. Daily mass of 42 nestling Zebra Finches in 12 asynchronous broods reared under food-abundant conditions. Dots represent single data points; numbers represent overlapping data points.

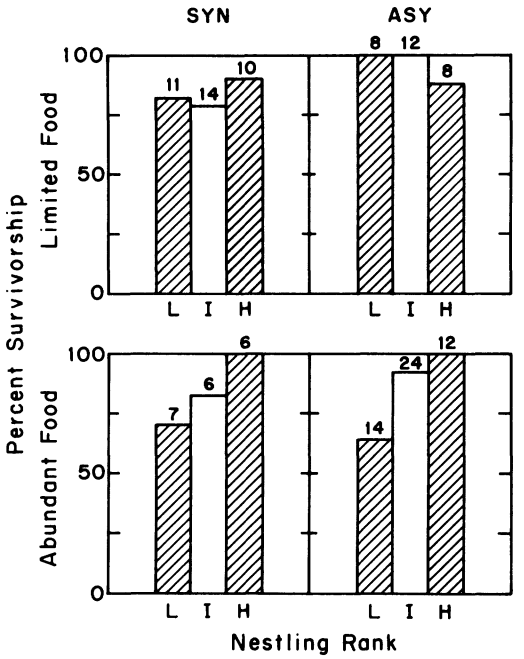

Fig. 5. Percentage survivorship of lightest (L) and heaviest (H) nestlings, and young intermediate in mass (I) in synchronous (SYN) and asynchronous (ASY) broods of food-limited and food-abundant treatments. Numbers above bars are sample sizes.

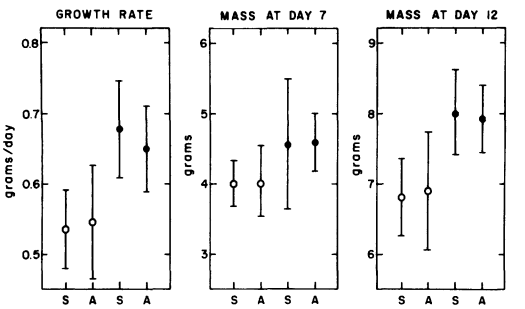

Fig. 6. Mean growth rate and nestling mass at 7 and 12 days of age of all Zebra Finches reared in synchronous (S) and asynchronous (A) broods under food-limited (open circles) and food-abundant (closed circles) conditions. Vertical lines represent 95% CI (mean ± 1.98 SE). Tests of significance for graphs from left to right are: $F_{3,110} = 3.90$, $P < 0.025$; $F_{3,110} = 2.17$, $P < 0.10$; $F_{3,110} = 4.11$, $P < 0.01$.

hierarchy.—The degree of hatching asynchrony did not significantly affect nestling survival and was not entered in the logistic regression model. Nine of 55 nestlings (16.4%) in synchronous broods and 8 of 77 nestlings (10.4%) in asynchronous broods died before fledging. There also was no difference in the age at mortality of young in synchronous (4.3 ± 3.02 days) and asynchronous (2.4 ± 2.26 days) broods ($t_{16} = 1.54$, $P > 0.10$).

Nestling rank within the brood hierarchy was the only variable that weakly influenced nestling survivorship according to the logistic regression analysis (deviance $\chi^2 = 5.159$, df = 2, $P = 0.076$). The heaviest nestlings were more likely to survive than those intermediate in mass, which in turn were more likely to survive than the lightest nestlings. This trend was significant among young of asynchronous broods when food was plentiful ($\chi^2 = 8.08$, df = 1, $P < 0.005$; Fig. 5). The same trend was present, although not statistically significant, among synchronous young when food was abundant ($\chi^2 = 1.99$, df = 1, $P > 0.10$). There was no differential survival by rank when food was scarce ($\chi^2 = 0.55$, df = 1, $P > 0.75$ for synchronous broods; $\chi^2 = 2.59$, df = 1, $P > 0.10$ for asynchronous broods).

When growth data for all nestlings, including young of intermediate rank, were examined in analyses of covariance, the degree of asynchrony had no significant effect on growth of nestlings in food-limited or food-abundant treatments. Growth rates and nestling mass at 7 and 12 days of age were similar between synchronous and asynchronous broods in both food-limited and food-abundant treatments (Fig. 6).

An interactive effect of asynchrony and rank in the brood hierarchy on growth of nestlings was apparent when only the heaviest and lightest brood members were used in paired comparisons tests. When food was limited, the heaviest young of asynchronous broods grew more quickly than their light siblings (Table 4), whereas there was no significant effect of rank on growth of young in synchronous broods. This same trend occurred in asynchronous broods when food was abundant, although the trend was not significant.

When food was limited there was a nonsignificant trend for heaviest siblings in asynchronous broods to grow faster than heaviest nestlings of synchronous broods (Fig. 7). Prefledging mass of heavy young in food-limited asynchronous broods was comparable to that of heavy young in all broods provided with abundant food, while heavy young in food-limited synchronous broods were considerably smaller at 12 days of age (Fig. 7).

TABLE 4. Growth parameters of lightest and heaviest nestlings in broods reared under conditions of limited (9 synchronous and 8 asynchronous) and abundant food (6 synchronous and 10 asynchronous broods).

		Lightest nestling	Heaviest nestling	Tests of significance of difference	
				t^a	P^b
Limited food					
Growth rate (g/day)	Syn	0.549 ± 0.128	0.551 ± 0.183	0.03	0.97
	Asy	0.531 ± 0.208	0.655 ± 0.156	3.36	0.012*
Mass at day 7 (g)	Syn	3.981 ± 0.713	4.158 ± 1.055	0.61	0.56
	Asy	3.760 ± 1.158	5.007 ± 0.946	5.35	0.000**
Mass at day 12 (g)	Syn	6.848 ± 1.322	6.923 ± 1.780	0.17	0.87
	Asy	6.922 ± 2.309	8.105 ± 1.300	2.40	0.047*
Abundant food					
Growth rate (g/day)	Syn	0.754 ± 0.132	0.710 ± 0.139	1.48	0.21
	Asy	0.621 ± 0.232	0.701 ± 0.225	1.20	0.26
Mass at day 7 (g)	Syn	4.742 ± 0.834	4.943 ± 0.962	0.96	0.39
	Asy	4.444 ± 1.546	4.931 ± 1.381	1.63	0.13
Mass at day 12 (g)	Syn	8.661 ± 1.002	8.429 ± 1.003	0.84	0.45
	Asy	7.961 ± 1.881	8.424 ± 1.567	0.96	0.36

[a] t-value from paired comparisons tests.
[b] * = $P < 0.05$, ** = $P < 0.01$.

Growth patterns of lightest siblings were different. Runts in asynchronous broods grew no more slowly than runts in synchronous broods when food was limited (Fig. 8). When food was abundant, runts in synchronous broods grew slightly but not significantly faster than those in asynchronous broods.

Effect of palate markings.—Nestling Zebra Finches have distinctive, dark, circular markings on their light-colored palates. These are common to the Estrildidae and are thought to play a role in parental feeding. Of 132 nestlings 18.9% lacked markings. Their palates were uniformly light in color. The absence of palate markings corresponded with white plumage in nestlings. Palate markings had no effect on nestling survivorship. With limited food these young grew more slowly (0.394 ± 0.196 g/day) than those with markings (0.581 ± 0.159 g/day; $F_{5,50} = 8.28, P = 0.006$). With abundant food there was no difference in growth of young with and without palate markings.

Effect of brood size.—Broods included in the analyses averaged 3.5 young (±1.11, range 2–6). Brood size did not differ between synchronous and asynchronous broods or between limited- and abundant-food treatments (Table 2). Brood size had no significant effect on survival of nestlings and thus did not enter the logistic regression model.

Under food-limited conditions, nestling growth correlated negatively with brood size. Young reared in broods of 2–3 nestlings grew more quickly (0.644 ± 0.143 g/day) than those in broods of 4–6 nestlings (0.422 ± 0.150 g/day; $F_{5,50} = 26.56$, $P < 0.001$). Brood size did not significantly affect growth rates or mass at day 7 when food was abundant but was negatively correlated with nestling mass at day 12 (regression coefficient = −0.912, $F_{5,52} = 5.91, P = 0.019$).

Effect of parental experience.—Nestlings reared by inexperienced parents suffered greater mortality (12 of 28 nestlings died; 43%) than nestlings reared by experienced parents (19 of 122 nestlings died; $\chi^2 = 10.282$, df = 1, $P < 0.001$). Some of these deaths (13) were unrelated to variables in this study and were eliminated from the data set used in subsequent analyses.

Experience of parents did not affect growth of young in food-limited treatments. When food was abundant, however, nestlings reared by inexperienced parents grew more quickly (0.887 ± 0.132 g/day, $n = 7$) than those reared by experienced parents (0.644 ± 0.178 g/day, $n = 56$).

Smaller nestling size results in smaller adult size.—Nestling mass at 12 days of age and adult mass were positively correlated for both males and females (Fig. 9). Females weighed more (12.350 ± 1.050 g) than males (11.836 ± 1.364 g) when they reached adulthood. Of 51 nestlings that attained less than the median mass (7.72 g) at 12 days of age and for which adult

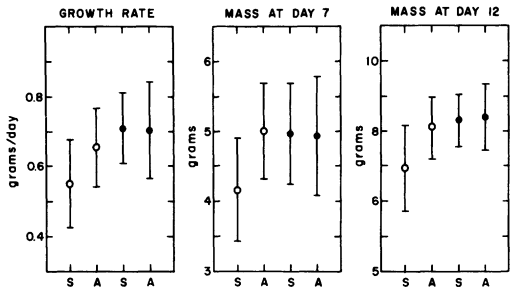

Fig. 7. Mean growth rate and nestling mass at 7 and 12 days of age of heaviest siblings of synchronous (S) and asynchronous (A) broods reared under food-limited (open circles) and food-abundant (closed circles) conditions. Vertical lines represent 95% CI (mean ± 2.04 SE). Tests of significance from left to right are: $F_{3,30} = 1.35$, $P > 0.10$; $F_{3,30} = 1.14$, $P > 0.10$; $F_{3,30} = 1.97$, $P > 0.10$.

mass was known, 69% were smaller than the median (12.06 g) at adulthood ($z = 2.71$, $P = 0.0068$, binomial test).

Parental loss of mass during the nestling period.—I weighed the parents at the completion of hatching and 12–14 days later in 27 nests. Females weighed significantly more than males at the beginning of the nestling period (13.183 ± 0.845 g for females, 12.319 ± 0.714 g for males; $t_{53} = 4.06$, $P < 0.001$) and lost a significantly greater percentage of their original mass than males (11.40 ± 4.696% vs. 7.03 ± 6.935%; $t_{53} = 2.91$, $P = 0.006$). Females lost a significantly larger percentage of their mass when food was limited than when food was abundant (13.28 ± 4.57% vs. 9.37 ± 4.06%; $t_{26} = 2.36$, $P = 0.027$),

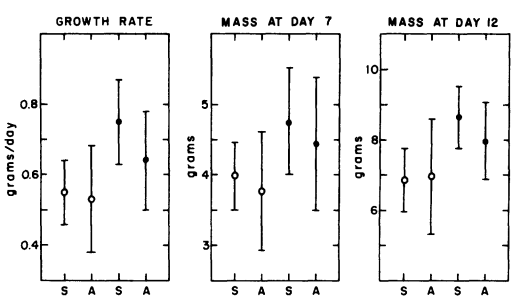

Fig. 8. Mean growth rate and nestling mass at 7 and 12 days of age of lightest siblings of synchronous (S) and asynchronous (A) broods reared under food-limited (open circles) and food-abundant (closed circles) conditions. Vertical lines represent 95% CI (mean ± 2.04 SE). Tests of significance from left to right are: $F_{3,29} = 1.82$, $P > 0.10$; $F_{3,29} = 0.99$, $P > 0.10$; $F_{2,29} = 1.71$, $P > 0.10$.

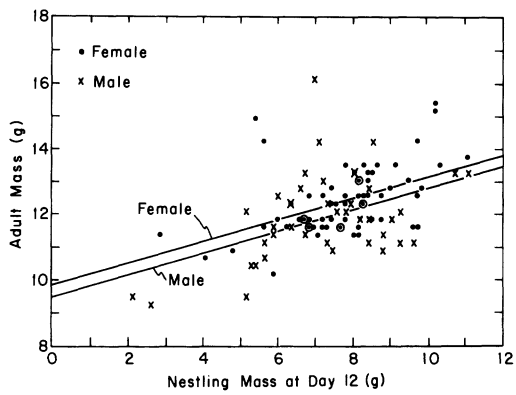

Fig. 9. Relationship of adult mass to prefledging mass (12 days of age) of male (×) and female (●) Zebra Finches. Lines represent best fits from linear regression analysis. $y = 9.37 + 0.341x$, $F_{1,38} = 10.56$, $P < 0.001$, $r^2 = 0.218$ for males; $y = 9.74 + 0.337x$, $F_{1,62} = 19.27$, $P < 0.001$, $r^2 = 0.237$ for females. Circled dots represent overlapping data points.

whereas male mass loss did not differ between treatments (8.03 ± 7.48% vs. 5.96 ± 6.42%; $t_{26} = 0.78$, $P = 0.45$). When food abundance and individual differences in original mass were taken into account, the degree of asynchrony had no effect on mass-loss patterns (percentage of original mass lost per day) of males ($F_{3,23} = 0.79$, $P > 0.50$) or females ($F_{3,23} = 0.01$, $P > 0.50$).

DISCUSSION

I found that Zebra Finch nestlings reared under conditions of abundant food grew more quickly than those in limited-food treatments. This finding is consistent with several experimental studies in which supplemental food was provided to breeding parents (Crossner 1977, Harris 1978, von Bromssen and Jansson 1980, Hogstedt 1981, Mock et al. 1987). I found no direct relationship between overall survival rates of young Zebra Finches and food abundance.

Asynchronous hatching facilitates differential growth and survival when food is scarce.—Growth patterns of nestling Zebra Finches supported prediction 1: late-hatching young were fed less than older siblings when food was scarce. When food was limited, heavy nestlings grew more quickly than their lightest nest mates in asynchronous but not in synchronous broods. Inequitable feeding of nestlings did not lead to higher mortality rates of the lightest siblings

under conditions of food scarcity. Evidence in support of prediction 2, that heavier nest mates in asynchronous broods fare better than those in synchronous broods when food is scarce, is essential for identifying an adaptive advantage to such differential growth. Although I observed a trend in the predicted direction, the findings were not statistically significant.

Contrary to prediction 3, that when food is plentiful there should be no differential growth and survival among nest mates, smallest siblings in asynchronous broods were at a disadvantage when food was abundant. Heaviest siblings grew more quickly, although not significantly so, and were significantly more likely to survive than their lightest siblings. Similarly, large size differences among nestlings precipitated mortality of 60% of the runts of House Martin (*Delichon urbica*) broods in spite of food abundance (Bryant 1978a, b). When fed abundantly, runts of asynchronous Zebra Finch broods grew slightly more slowly than those of synchronous broods, suggesting that the lightest nestling would be favored by a more synchronous hatching pattern when food is abundant. Brood reduction, therefore, may be a maladaptive consequence of asynchronous hatching when food is plentiful (Bryant 1978a, b; Clark and Wilson 1981).

Parental feeding and begging behavior.—The feeding hierarchy that led to differential growth and survival of Zebra Finches in broods provided with abundant food may have been created by parental decisions about (1) the rate at which nestlings should be fed and (2) the distribution of food among nestlings. Nestlings signal their food needs by begging more vigorously when hunger levels are greater (von Haartman 1949, Nottebohm and Nottebohm 1971, Henderson 1975, Ryden and Bengtsson 1980, Bengtsson and Ryden 1983, Fujioka 1985, Mock and Ploger 1987). By varying rates of food delivery in response to the intensity of vocal begging signals of the brood, parents seem to adjust their feeding rate to the average hunger level of the brood rather than to that of the hungriest nestling (Bengtsson and Ryden 1983). Fujioka (1985) noted that Cattle Egrets (*Bubulcus ibis*) stopped feeding young when only one member of a brood begged. Even with abundant food, a feeding hierarchy would be created if parents adjust their feeding rates to average brood hunger and preferentially feed the oldest or largest nestlings. Some parents feed the nestling that provides the largest, closest, or most conspicuous target (*Parus major* and *Turdus pilarus*, Ryden and Bengtsson 1980; *Melospiza melodia*, Reed 1981; *Fulica americana*, Horsfall 1984; male *Melopsittacus undulatus*, Stamps et al. 1985; *Dumetella carolinensis*, Skagen unpubl. data; but see Stamps et al. 1985 regarding female *Melopsittacus undulatus*). If Zebra Finch preferences are based on similar cues, and if the preferred chicks are also the largest brood members, then a size-based hierarchy could be produced. If older young are fed preferentially on each nest visit, late-hatched nestlings may be unable to obtain adequate food for survival in spite of abundant food.

The lack of differential mortality of young Zebra Finches by relative size when food was scarce suggests that food distribution was more equitable than when food was abundant, but was probably due to the experimental feeding procedures used. Adult Zebra Finches of food-limited treatments were given seed at 3–6 h intervals, and at times food was temporarily depleted. When food was replenished these parents fed their young immediately and rapidly; therefore, the runts as well as older nestlings received a large amount of seed. These periodic large meals may have prevented death by starvation of the lightest nestlings. I inferred the rate of food delivery from the amount of seed contained in the esophageal diverticula of nestlings shortly after feedings. The amount of seed fed to young of food-limited broods 30–60 min after food was replenished far exceeded that given to food-abundant broods during comparable time periods. Seed stored in the esophageal diverticulum of food-limited nestlings ranged up to 30% of their mass.

Greater levels of food deprivation than in this study might produce greater nestling mortality. In nature we might expect differential survival of the nestlings when food is limited. Unlike the temporal nature of seed availability in an aviary experiment, sudden flushes in available seed after temporary scarcity may be less likely to occur in the wild (e.g. only if seed is patchily distributed and quickly depleted).

An alternative explanation for low survival rates of runts when food was abundant is that nestling mortality is related to intrinsic differences in offspring quality. One would then expect similar patterns of mortality in food-limited and food-abundant treatments, which I did not find.

Implications of nestling condition for adult size.—Zebra Finch nestlings that were small before fledging were likely to be small as adults, even though postfledging food supplies were abundant. Ricklefs (1984) concluded that growth rates of nestling European Starlings (*Sturnus vulgaris*) reflect aspects of parental care rather than genotypic factors or egg composition, but he postulated that final size at adulthood is due primarily to genetic factors. In Zebra Finches parental care during the nestling period can contribute significantly to adult size. Similarly, Boag (1987) reported experimental evidence that the quality of nestling diet significantly influences several morphological features of Zebra Finches at adulthood. In a natural setting larger adult size in turn may influence postfledging survival (Perrins 1965, Jarvis 1974) and future breeding success (Lundberg et al. 1981).

Parental loss of mass and body condition.—To maximize lifetime reproductive output parents must balance the time and energy investments in current and future breeding efforts (Trivers 1974, Stearns 1976) by ensuring high fledging mass of as many young as possible while maintaining a healthy physical condition. Increased feeding rates may, but do not always, lead to faster growth and higher survival rates of young (Bengtsson and Ryden 1983, Stamps et al. 1985). Many parents can provision young at a greater rate than they typically do (Harris and Plump 1965, Loman 1980, Richter 1984, Mock and Ploger 1987). Although parents may reach an upper limit for energy expenditure, estimated at 3.9–4.0 BMR (Utter and Lefebvre 1973, Drent and Daan 1980), sustained performance above an "optimal working capacity" (Royama 1966) may expose parents to increasing risks of fatigue or predation. Greater reproductive effort is associated with greater loss of mass and decreased survival in adults (Nur 1984) and lower success of later nesting attempts (Slagsvold 1984, Roskaft 1985). In the Zebra Finch experiments mass-loss patterns of females but not of males were sensitive to food abundance, suggesting sexual differences in response to such stress.

The evidence reported here is not as clear as one would expect if Lack's hypothesis described the primary advantage of asynchronous hatching. When food abundance was low, a size hierarchy among young promoted differential growth and survival of early- and late-hatched young, as Lack suggested, but beyond this the evidence was equivocal. Similarly, only a few of several recent experimental studies examining Lack's hypothesis reported supportive evidence. Hahn (1981) reported that asynchronous broods of Laughing Gulls (*Larus atricilla*) had greater fledging success than synchronous broods. Husby (1986) replaced young in Black-billed Magpie (*Pica pica*) nests where mortality had occurred and found that although parents could successfully raise all young to fledging, these broods experienced higher postfledging mortality than control broods. Slagsvold (1986) reported higher fledging mass in asynchronous than in synchronous broods of Pied Flycatchers (*Ficedula hypoleuca*). The majority of these experimental studies do not support the adaptive value of asynchronous hatching that Lack proposed with regard to numbers of young fledged, or growth rates and fledging mass of surviving young in asynchronous and synchronous broods (Werschkul 1979; Slagsvold 1982, 1985, 1986; Fujioka 1985; Shaw 1985; Haydock and Ligon 1986; Mock and Ploger 1987; Amundsen and Stokland in press; Skagen 1987).

Alternative explanations for asynchronous hatching, such as reducing sibling rivalry (Hahn 1981), reducing nest predation (Hussell 1972, 1985; Clark and Wilson 1981), or expanding the period of peak food demand by nestlings (Hussell 1972), may be more applicable to Zebra Finches. Asynchronous hatching may be one of several possible responses to a complex suite of avian reproductive challenges, and may have evolved for different reasons in different groups of birds (Slagsvold et al. 1984).

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