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HATCHING ASYNCHRONY IN AMERICAN GOLDFINCHES: AN EXPERIMENTAL STUDY[1]

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Abstract. I examined Lack's (1954, 1968) hypothesis that asynchronous hatching is an adaptive response to food shortage during the breeding season by comparing growth and survival of nestlings in asynchronous and artificially created synchronous broods of American Goldfinches (*Carduelis tristis*). I also examined the effects of seasonal and environmental factors on nestling growth and survival and on hatching asynchrony.

Nestlings in asynchronous broods were more likely to diverge in mass and did so at a faster rate than those in synchronous broods. The lightest nestlings of asynchronous broods grew more slowly than their heavier nestmates and than all nestlings in synchronous broods. Brood reduction occurred more frequently in asynchronous broods. Survival and growth rates decreased throughout the breeding season and during inclement weather. Hatching intervals increased during the season.

When brood reduction or differential growth among nestmates occurred in asynchronous broods, suggesting that the energy available for growth was limiting, heavy nestlings in asynchronous broods grew nonsignificantly faster than heavy nestlings in concurrent synchronous broods. This trend implies that when insufficient food is delivered to nestlings, asynchronous hatching may provide a slight advantage for older nestlings.

Growth rates of all nestlings, however, were greatest in highly synchronous broods. Explanations other than growth of young must be invoked to explain why extreme synchrony is not more common in goldfinches. I discuss constraints on the normal pattern of hatching asynchrony characteristic of this species. The proximate mechanism for differential feeding and brood reduction is discussed.

Key words: American Goldfinch; Carduelis tristis; *growth; hatching asynchrony; size hierarchy; survival.*

INTRODUCTION

Eggs of many altricial species of birds do not hatch synchronously, but rather hatch asynchronously over a period of one or more days (Clark and Wilson 1981). Many ideas have been proposed to explain the adaptive nature of asynchronous hatching, the most widely invoked being those of Lack (1954, 1968). Lack theorized that asynchronous hatching is an adaptive response to food shortages. A disparity in the ages of nestlings results in a dominance hierarchy among siblings, and the youngest sibling receives less food. Under conditions of food scarcity, the lightest nestling would be rapidly eliminated, and the probability of survival of the remainder of the brood would increase.

Alternative views of the possible adaptive basis for asynchronous hatching include the "predation" or "nest failure" hypothesis (Clark and Wilson 1981), which suggests that asynchronous hatching reduces the probability of total brood loss by predation. The "peak demand reduction" hypothesis (Hussell 1972, Bryant 1978*b*) proposes that asynchronous hatching is a means of reducing the workload of parents at the time of peak food demand by nestlings. Hamilton (1964) and Hahn (1981) propose that asynchronous hatching, by imposing a size hierarchy, could reduce sibling rivalry, the "sibling rivalry reduction" hypothesis. Further, Mead and Morton (1985) suggest that asynchronous hatching is a condition that is physiologically imposed by the hormonal mechanism governing egg laying and incubation. Although synchronous hatching and brood reduction are widespread among altricial species, the relative importance of these various hypotheses is largely unknown and may differ among different groups of birds (Slagsvold 1986*b*).

I examined Lack's hypothesis in a temperate open-nesting passerine, the normally asynchronous American Goldfinch (*Carduelis tristis*). I artifically created synchronous hatching by switching young of different ages between nests. I thus was able to compare survival and growth of "synchronous" broods with "asynchronous" broods. I explored Lack's hypothesis at three levels. The first two predictions are primarily descriptive, asking if hatching asynchrony promotes differential growth and/or brood reduction. Support for prediction 3 would further suggest that such differential growth or survival is adaptive. And finally, the fourth prediction would be supported if the primary adaptive value of hatching asynchrony were to provide optimal conditions for

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growth and survival of young. I examined the following predictions. (1) A size hierarchy at hatching facilitates differential feeding of young; chicks in asynchronous broods diverge in mass more quickly than those in synchronous broods. (2) Late-hatching nestlings in asynchronous broods are more likely to die or to grow more slowly than their nestmates than are late-hatching chicks in synchronous broods. (3) Growth rates of older nestlings improve as a result of mortality or slowed growth of the lightest member of the brood. (4) The normal pattern of hatching reflects the optimal conditions for growth and survival of young; broods approximating the modal degree of asynchrony grow more quickly and attain higher prefledging masses than broods of greater synchrony or asynchrony than is normal for the population.

This study also examines additional biological and environmental factors that influence growth and survival of young, and identifies factors that contribute to the establishment of size hierarchies.

Methods

Experimental animal and study site

I studied nesting goldfinches during July–September 1983 and 1984, at the Leopold Memorial Reserve, Sauk County, southcentral Wisconsin. Here goldfinches build small, open-cup nests in shrubs, primarily dogwood (*Cornus* spp.) and willow (*Salix* spp.), which are bordered by sedge meadow and hardwood forest. Goldfinches are granivorous during the breeding season and feed their young by regurgitating partially digested seeds. Primary foods (based on observations of foraging parents during the nestling period) included seeds of thistle (*Cirsium vulgare, C. discolor, C. arvense,* and *Carduus aeanthoides*), grasses (*Phalaris* spp., *Phleum* spp.), mullein (*Verbascum blattaria*), goatsbeard (*Tragopogon* spp.), and gayfeather (*Liatrus pycnostachya*). Nestlings temporarily store seed in esophageal diverticula, or false crops, and seed can be observed through the transparent neck skin. Based on these observations, I discerned that parents also fed their young insect larvae and pieces of green vegetation.

Procedures

Goldfinch nests were monitored at 0.5–3 d intervals to determine date of hatching and fate of nest ($N = 51$ nests in 1983 and 121 in 1984). During the hatching period, I attempted to visit nests twice daily. Desertion, predation, and use of nests for other experiments reduced the number of nests used in this study to 16 in 1983 and 57 in 1984.

At the time of hatching, nests were randomly assigned to "synchronous," "asynchronous," and "control" treatments. Treatment assignments were made in a stratified manner to control for weather, time of season, and brood size. Recently hatched nestlings (ages 0–5 d) were transported in protective containers to assigned nests to establish broods with young of nearly equal size and age (synchronous) and broods with young of unequal size and age (asynchronous). Twenty and 156 young were moved in 1983 and 1984, respectively. Transfers averaged 14.9 min in duration (±12.44 min, range 3–50). Because parents bring food to their broods at an average rate of 2.3 trips/h (S. K. Skagen, *personal observation*), the duration of transport of nestlings probably did not adversely affect young. Nestlings in control nests were removed for weighing and measuring, and were returned to their original nests.

Nestlings were weighed (±0.01 g; Ohaus triple beam balance) at 1–3 d intervals. To adjust for variation in nestling mass during the day, 32 nestlings in 11 nests were weighed 3–6 times daily at 1–3 d intervals. Rates of growth during the day were determined using linear regression on these repeated measures. The percent of noon mass was then predicted for each hour of the day, and all mass records were adjusted to "noon mass."

During nest visits, wing chord and tarsus measurements (±0.1 mm; dial vernier calipers) were also recorded. The amount of food stored in the esophageal diverticulum was estimated, using a ranking scale from 0 (empty) to 4 (full). Nestlings were individually marked with various colors of nail polish on back toenails. Nest visits, requiring 5–10 min, were continued until fledging, nest destruction, or brood day 12 (the day the first nestling in a brood hatched was considered brood day 0 for that brood). Young that were absent from the nest when > 10 d old were considered to have "fledged" (young normally fledged between 10–16 d of age). Mortality was attributed to "starvation" if nestlings showed a reduced rate of mass gain or actual mass loss before disappearing. To determine hatching mass, eight nests were checked 2–5 times daily during hatching, and the condition of down (wet, slightly matted, or dry) was noted for all newly hatched young.

Data analyses

Growth rates, based on changes in mass from 1 to 10 d of age, were estimated by linear regression, and the slope of the line of best fit was used as an indicator of growth by which to compare individuals. Coefficients of determination (r^2) of 97% of the observations exceeded 90%; 70% of the observations exceeded 98%, indicating that the linear model is appropriate to describe growth between ages 1 and 10 d. Parameters described by growth curves that require specification of an asymptote, such as the logistic model (Ricklefs 1967), are highly sensitive to the value specified. I did not use such curves to describe growth of individual nestlings because I could obtain little information on asymptotic masses.

Precise hatching times are difficult to determine for all nestlings, and more frequent visits to nests during hatching may result in undue disturbance. I therefore used another method, also used by Slagsvold (1986*a*),

in estimating the relative age differences between nestmates. I used the relative sizes of siblings (heaviest, lightest, intermediate in mass and wing chord) as an indicator of their hatching order (first-hatched, last-hatched, intermediates). I believe this approach is a valid way to determine relative age differences among nestmates because average within-brood variances in hatching mass and wing chord are small (0.016 g and 0.059 mm, respectively, $N = 8$ broods), and nestling goldfinches grow on average 0.79 g their first day posthatching. First- and last-hatched nestlings are therefore easily distinguished from each other and generally from intermediates by relative size.

Stepwise multiple regression analyses were used to determine the influence of several independent variables on the growth rates of nestlings. Relative ranks (heaviest coded as 3, lightest coded as 1, intermediates coded as 2) of nestmates were assigned based on relative mass and winged chord measurements at hatching. Dates from 22 July to 9 September were assigned values of 1–50 to represent seasonal trends. Weather conditions were classified as cold, rainy conditions (coded as 1, and defined by the combination of low temperatures [minimum daily temperature < 16°C] and high rainfall [> 2 cm during the 1st wk posthatching]) and normal conditions (coded as 0). Weather information was obtained from daily temperature (minimum and maximum) and precipitation records maintained by C. Bradley, Leopold Memorial Reserve. Growth data was also classified by year, 1983 (coded as 0) and 1984 (coded as 1).

I tested the robustness of multiple regression analysis to violation of the assumption of independence of data (individual young from the same brood cannot be assumed to be independent) in two ways. First, I randomly selected one member of each brood to form a subset of the entire data set, and second, I calculated mean response variables (growth rates and mass at 10 d of age) for each brood. Because analyses of these data sets revealed the same major trends as multiple regression analyses of the data set that includes all individual nestlings, I report results of the most inclusive analyses.

Where growth data and residuals about the regression line appeared to be negatively skewed, growth rates were transformed to e^y where y is growth rate. Because the results of analyses using this transformation did not differ markedly from the same analyses using untransformed data, only the latter results are reported.

Growth parameters describing mass, wing chord, and tarsal development of treatment groups were determined using Richards' curve (Bradley et al. 1984). For these analyses, asymptotic values of 13 g, 60 mm, and 17 mm were used for mass, wing chord, and tarsal measurements, respectively.

The difference in nestling mass (DNM = mass of heaviest − mass of lightest brood member) and the relative difference in nestling mass (RDNM = DNM/mean mass of brood members) were used to describe the size hierarchy at hatching (initial, at completion of hatching), at the beginning of the treatment (when brood manipulations were performed), and 6 d (range 5–7) after treatments began. Data for young > 10 d old were not included in these analyses because some growth curves levelled off after that age. Those broods in which RDNM was < 0.45 were considered synchronous treatments, and asynchronous treatments were those in which RDNM exceeded 0.45 (Fig. 1). The effects of brood size, RDNM at treatment, time in season, and year on the rates of divergence in mass of nestmates (change in DNM [grams per day] for a 6-d period after treatment began) were examined using stepwise multiple regression. Only broods that did not experience nestling mortality and in which treatments began by brood day 4 were used in this analysis.

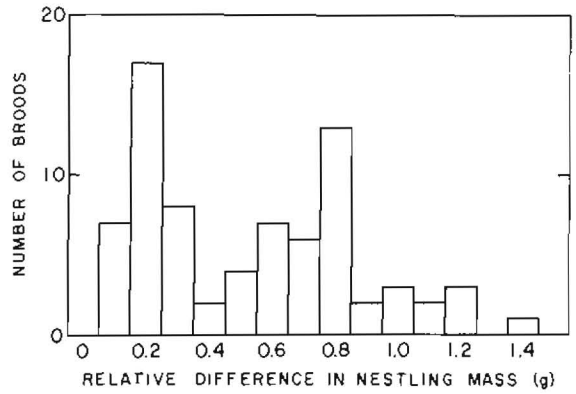

FIG. 1. Distribution of size differences among nestmates [RDNM, Relative Difference in Nestling Mass = (range of nestling masses in brood)/(mean mass of brood members)] after experimental brood manipulations in 33 synchronous (RDNM < 0.45) and 39 asynchronous (RDNM > 0.45) broods of American Goldfinches.

Statistical analyses were performed by Minitab (Ryan et al. 1976) and SPSS (Nie et al. 1975, SPSS 1983). Variation about the mean is reported as $\bar{X} \pm$ SD, unless specified otherwise. Results were considered significant at the .05 level.

RESULTS

Growth and survival of 341 nestlings in 73 nests were monitored in 1983 and 1984. Twenty-five cases of nestling mortality were attributed to causes other than predation. Ten young in eight nests died of starvation, and 10 young in two nests died of exposure during cold, rainy weather. Other suspected causes of mortality included falling out of unstable nests (2), trampling (2), and destruction by marsh wrens (*Cistothorus palustris*) (1).

At the the time of brood manipulations (beginning of treatment; brood day 2–3 for control nests), there were no significant differences in brood size, brood day,

TABLE 1. Descriptive statistics (mean ± SD) of characteristics of synchronous, asynchronous, and control broods at the time of brood manipulations (beginning of treatment).

Variable	Treatment		
	Synchronous	Asynchronous	Control
Number of broods	30	28	15
Number of nestlings	140	128	73
Mean RDNM*	0.20 ± 0.07	0.81 ± 0.21	0.72 ± 0.29
Mean hatch period (d)	0.5 ± 0.57	2.3 ± 0.70	2.0 ± 1.13
Brood size†	4.7 ± 0.80	4.6 ± 1.00	4.9 ± 0.83
Brood day‡	2.3 ± 0.84	2.9 ± 0.96	2.5 ± 1.41
Mean mass (g)§	2.88 ± 0.84	2.64 ± 0.76	2.41 ± 0.73
Percent of nestlings moved	68.6	63.3	0

* Relative difference in nestling mass = (range in nestling body masses within brood)/(mean body mass of nestlings in brood).
† $F_{2,70} = 0.58$, $P > .50$.
‡ $F_{2,70} = 2.20$, $P > .20$.
§ $F_{2,70} = 1.74$, $P > .20$.

or mean mass of young in synchronous, asynchronous, or control groups (Table 1). At the beginning of treatments, size differences among nestmates (RDNM) of asynchronous broods were similar to that of control broods (Table 1). No young in control nests were transplanted to other nests; similar proportions of young in the two experimental groups were moved to other nests (Table 1). There were no significant differences between treatment groups in timing of breeding during the season ($F_{3,69} = 0.71$, $P > .50$) or year ($F_{3,69} = 1.05$, $P > .50$).

The numbers of goldfinches in the broods ranged from 3–7. The average number in broods in which 1 or more young died of starvation was significantly higher (5.5 ± 0.93, range 4–7) than the average number in the remainder of the broods (4.5 ± 0.79, range 3–7; $t_{71} = 2.84$, $P < .01$). Brood size had no apparent effect, however, on the growth rates of surviving young (partial $F_{1,330} = 0.21$, $P > .50$). For this analysis, variables entered in the model were brood size, rank in brood, RDNM, time in season, weather, and year. Brood size was omitted from subsequent analyses.

To determine possible effects of brood manipulations, I compared growth rates of 104 nestlings that were returned to their original nests at the time of brood manipulations with 156 that were transported to other nests in 1984. There was no difference between the growth rates of nestlings in these two groups ($t_{265} = 0.97$, $P > .20$). In addition, growth rates of 73 nestlings in control nests were no greater than those of 268 nestlings in experimental nests ($t_{337} = 0.97$, $P > .20$). Because there were no differences in growth rates due to moving young between nests, control broods were combined with experimental treatment groups in subsequent analyses.

TABLE 2. Factors significantly influencing the growth rates and mass at 10 d of age of nestling goldfinches as determined by multiple regression analyses.

Variable	Coefficient	Partial F value	P
Growth rates of nestlings*			
Rank in brood	0.013	0.194	NS
RDNM†	−0.345	12.041	<.001
Rank × RDNM interaction	0.149	9.923	<.001
Time in season	−0.005	29.485	<.001
Weather	−0.139	8.703	<.001
Year	0.074	6.003	<.001
Nestling mass at age 10 d‡			
Rank in brood	0.250	0.81	NS
RDNM	−3.080	10.89	<.001
Rank × RDNM interaction	1.245	7.84	<.001
Time in season	−0.047	27.77	<.001
Weather	−1.224	11.49	<.001

* $r^2 = 0.266$, df = 6, 331.
† Relative difference in nestling mass = (range in nestling body masses within brood)/(mean body mass of nestlings in brood).
‡ $r^2 = 0.225$, df = 5, 332.

Seasonal and environmental factors

The time during the breeding season at which nestlings hatched significantly influenced growth rates (Table 2). The first eggs were laid on 15 July 1983 and 8 July 1984, and the first young hatched on 31 July and 22 July, respectively. The latest nests included in the sample held the first egg on 23 August 1983 and 31 August 1984, and first young on 3 and 6 September, respectively. Growth rates declined as the season progressed; young that hatched later in the season grew more slowly than those hatched earlier (Table 2, Fig. 2). Starvation occurred only in the latter half of the season (after 13 August). In addition, young grew faster in 1984 than in 1983 (Table 2), averaging 0.831 (±0.237 g/d in 1983 and 0.957 ± 0.207 g/d) in 1984.

Weather conditions significantly influenced growth rates of young (Table 2). Growth rates of nestlings exposed to cold, rainy conditions on at least 2 d of their 1st wk posthatching averaged 0.697 ± 0.276 g/d (N = 30), whereas nestlings not exposed to such conditions grew 0.950 ± 0.163 g/d (N = 306). There were two cold and rainy spells 3–5 d in duration during the 1983

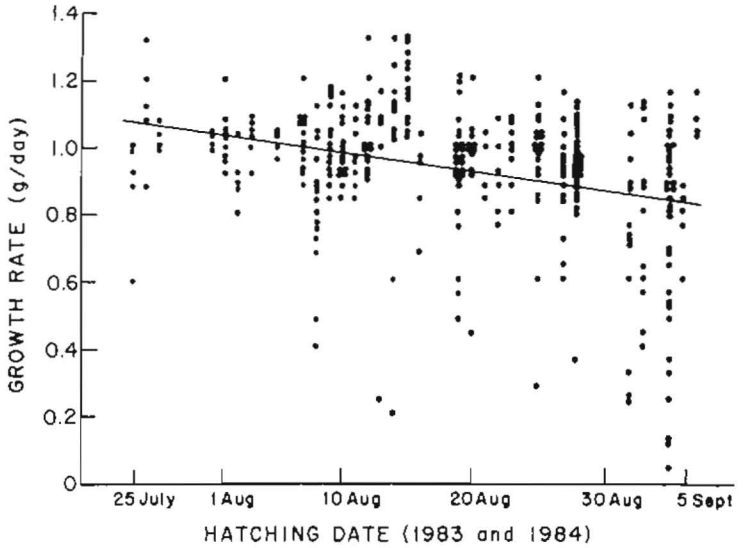

FIG. 2. Growth rates (grams per day) of nestling goldfinches in broods hatching at different times during the breeding season. Line represents line of best fit from linear regression, $Y = 1.11 - 0.006x$ ($F_{1,337} = 40.069$, $P < .001$, $r^2 = 0.104$). For analysis, 22 July–9 September were assigned values of 1–50.

season and none in 1984. During July, August, and September, total rainfall in the study area was greater in 1983 (32.7 cm) than in 1984 (21.0 cm). Temperatures ranged from a minimum of 7° to a maximum of 36°C.

Establishment of size hierarchies

Eggs in a goldfinch clutch normally hatch asynchronously. Hatching periods (number of days required for a clutch to hatch completely) were determined for 66 broods and averaged 1.9 ± 0.680 d (range 0–4), and RDNM within 1 d of the completion of hatching averaged 0.641 ± 0.227. In accordance with the working definition of asynchrony used in this study (RDNM > 0.45), 80.3% (53 of 66) of the broods were asynchronous (Fig. 3). The effects of hatching period, brood size, and differences in mass among hatchlings on the size hierarchy within 1 d of the completion of hatching and before brood manipulations were examined in 66 nests.

Differences in mass (DNM and RDNM) were highly correlated with hatching periods (Table 3). Hatching periods in turn varied positively with brood size (partial $F_{1,63} = 16.89$, $P < .001$; Tables 3 and 4) and with progression of the breeding season (partial $F_{1,63} = 5.11$, $P < .05$). This trend was not, however, related to changes in clutch size; there were no seasonal trends in clutch size in 1983 ($F_{1,22} = 0.49$, $P > .50$) or in 1984 ($F_{1,63} = 0.35$, $P > .50$).

I examined mass and body measurements recorded within 6 h of hatching of 68 nestlings to determine the effect of hatchling size on size hierarchies established at hatching. Because natal down of hatchlings is wet and matted, requiring 3–6 h to dry, I could estimate hatching time by the condition of the down of a sample of hatchlings or by the status of the egg at a nest check <6 h earlier. Hatchlings weighed on average 1.12 ± 0.117 g (range 0.89–1.41, $N = 68$). Wing chord and tarsus measurements averaged 5.6 ± 0.30 mm ($N = 64$) and 5.2 ± 0.33 mm ($N = 45$) at hatching, respectively. Only 1 of 68 hatchlings had recently been fed, as indicated by the presence of seeds in its esophageal diverticulum.

In 14 nests, I recorded hatchling mass for 2–5 siblings. Hatchling mass increased with the order of hatching in 11 of these nests, and mass decreased with order of hatching in 2 nests. At the time of hatching, the youngest nestlings weighed on average 114% (range

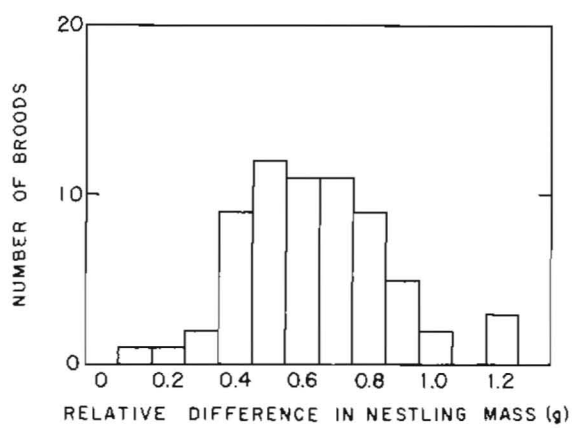

FIG. 3. Distribution of initial size differences among nestmates [RDNM, Relative Difference in Nestling Mass = (range of nestling masses in brood)/(mean mass of brood members)] in 66 broods of American Goldfinches before experimental brood manipulations.

TABLE 3. Correlation matrix (r) for clutch and brood sizes, hatching periods (d), and mass difference measures (DNM and RDNM)† within 1 d of completion of hatching (before brood manipulations) of 66 goldfinch broods.

	Clutch size	Brood size	Hatching period	DNM
Brood size	0.768***			
Hatching period	0.267*	0.428***		
DNM	0.299*	0.448***	0.737***	
RDNM	0.320**	0.472***	0.775***	0.853***

* $P < .05$, ** $P < .01$, *** $P < .001$ (significance level of correlations).

† DNM = range in nestling body masses within brood; RDNM = (DNM)/(mean body mass of nestlings in brood).

105–125%, $N = 8$ nests) of the hatching mass of their oldest sibling. Based on an estimate of the instantaneous growth rate of 1-d-old nestlings (0.79 g/d: S. K. Skagen, *personal observation*), the larger size of late-hatching young is equivalent to advancing the time of hatching by 3 h.

Prediction 1: Does a size hierarchy at hatching facilitate differential growth of young?

Sixty-one broods experienced no nestling mortality. In these broods, the heaviest and lightest brood members diverged in mass (change in DNM [grams per day] for a 6-d period after treatment began) at an average rate of 0.21 ± 0.176 g/d (median = 0.18, range = −0.095–0.863). Rates of divergence in mass were positively correlated with RDNM at the beginning of the treatment ($F_{1,60} = 5.47$, $P < .01$). In only 8 of 26 synchronous broods, divergence in mass exceeded the median rate, whereas 23 of 35 asynchronous broods diverged in mass more quickly than the median rate ($\chi^2 = 7.171$, df = 1, $P < .001$). The same model also revealed that broods diverged in mass more quickly as the season progressed (partial $F_{1,58} = 9.55$, $P < .01$). However, according to a more inclusive model (with brood size, year, and number of days of growth added), neither brood size (partial $F_{1,55} = 0.06$, $P > .50$) nor year (partial $F_{1,55} = 1.69$, $P > .25$) significantly influenced rates of size divergence.

Broods were then assigned to four groups based on RDNM at the beginning of treatment (RDNM < 0.45 for synchronous and RDNM > 0.45 for asynchronous) and rates of divergence in mass ("parallel" broods diverged more slowly than 0.18 g/d, and "diverging" broods exceeded 0.18 g/d). There were no differences between groups in brood size or in mean mass of young at the beginning of treatments (Table 5).

Young in asynchronous diverging broods diverged in mass more quickly than those in synchronous diverging broods ($t_{30} = -2.19$, $P < .05$; Table 5). Six days after treatments began, differences in mass (final DNM) of the diverging synchronous broods were equivalent to the original size differences of asynchronous broods (Table 5).

Mean mass gain of young (grams per nestling per day) differed significantly between two of these groups ($F_{3,57} = 4.18$, $P < .01$; Table 5); mean mass gain in parallel asynchronous broods was greater than that in diverging asynchronous broods ($q_{57,4} = 4.87$, $P < .01$, Student-Newman-Keuls multiple range test). There were no differences in mass-gain patterns between synchronous parallel and diverging broods, or between synchronous broods and asynchronous broods.

If one assumes that mass-gain patterns reflect the energy available for growth (E_{growth}), and this in turn reflects the overall quality and amount of food delivered to nestlings, then one can compare the rates of divergence in nestling mass between synchronous and asynchronous broods in relation to food provisioning by parents. I also assumed that there were no differences between synchronous and asynchronous broods in growth efficiencies of young (megajoules in new tissue/megajoules eaten) nor in food quality in regard to energy content. The median daily mean mass gain (0.96 g/d) was used to delineate conditions of relatively low and high E_{growth}. When E_{growth} was high, the number of parallel and diverging broods was independent of original size differences (synchronous or asynchronous) (Fisher exact probability test, $P > .20$). However, when E_{growth} was low, most (15 of 18) asynchronous broods diverged, whereas only 6 of 13 synchronous broods diverged (Fisher exact probability test, $P < .05$).

Prediction 2: Do late-hatching young in asynchronous nests grow more slowly than other young?

Nestlings died of starvation in 6 of 41 (14.6%) asynchronous broods and in 2 of 33 (6.1%) synchronous broods ($\chi^2 = 2.018$, df = 1, $P > .20$). Collectively,

TABLE 4. Hatching period, DNM, and RDNM* (means ± SD) of broods of different sizes, within 1 d of completion of hatching (before brood manipulations).

Brood size	N	Hatching period (d)	DNM (g)	RDNM (g)
All	66	1.9 ± 0.68	1.473 ± 0.783	0.641 ± 0.227
3	6	1.2 ± 0.75	1.008 ± 0.608	0.421 ± 0.171
4	23	1.6 ± 0.78	1.247 ± 0.473	0.571 ± 0.157
5	32	2.1 ± 0.82	1.585 ± 0.730	0.703 ± 0.227
6	4	2.5 ± 1.00	1.790 ± 1.040	0.778 ± 0.320
7	1	3	4.64	1.049

* DNM = range in nestling body masses within brood; RDNM = (DNM)/(mean body mass of nestlings in brood).

growth rates of nestlings in synchronous broods (0.943 ± 0.210 g/d) did not differ from those of young in asynchronous broods (0.920 ± 0.218 g/d; $t_{340} = 0.96$, $P = .34$). Multiple regression analysis revealed several factors that were significantly correlated with rates of growth and development of nestlings (Table 2). The interaction of an individual's rank in the brood ("heaviest," "intermediate," or "lightest") and differences in mass (RDNM) at the beginning of treatment significantly influenced both growth rates and nestling mass at 10 d of age (Table 2). The lightest nestlings in asynchronous broods grew more slowly than all other nestlings, whereas there were no statistical differences among all other young in both synchronous and asynchronous broods (Fig. 4). The lighest nestlings in synchronous broods grew more slowly than their siblings, but this trend was not significant. A similar trend was exhibited by nestling mass at 10 d of age.

In contrast to the nestling's rank after brood manipulations, there was no difference in growth rates attributable to a nestling's rank in its original (natal) nest ($F_{2,53} = 2.13$, $P > .20$; $F_{2,144} = 0.98$, $P > .50$; $F_{1,53} = 1.40$, $P > .20$ for lightest, intermediate, and heaviest young, respectively; 1984 data only).

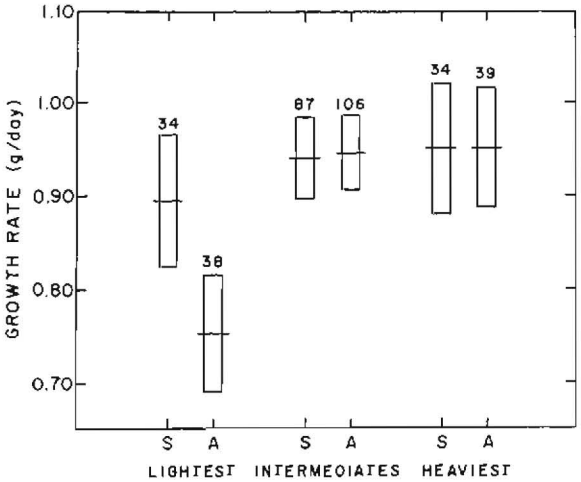

FIG. 4. Growth rates (grams per day) of lightest nestling, heaviest nestling, and one or more young intermediate in the size hierarchy in 34 synehronous (S) and 39 asynchronous (A) broods. Horizontal lines represent means and vertical bars delineate 95% CI (mean ± 1.968 SE). Sample sizes appear above the bars. Data are included only on individuals for which growth rates could be determined; a growth rate could not be determined for lightest member of one asynchronous brood.

Prediction 3: Is there a benefit for larger nestmates?

Lack's hypothesis suggests that selective starvation of the lightest nestling would result in faster growth rates or higher fledging masses of older siblings. To examine this idea, I selected from the total sample asynchronous broods that either experienced brood reduction or in which growth rates of the heaviest and lightest young differed (slopes of regression lines differed at the $P < .10$ level). I then paired these 14 broods with synchronous broods that did not experience differential growth of nestlings and that hatched at the same time (within 1 d). I assumed that broods being reared at the same time of the season experienced the same weather and food availability conditions; I could not address possible differences in parental quality, however. Growth rates and mass at 10 d of age of the heaviest and intermediate young in these nests were then compared between paired nests.

The heaviest and second heaviest nestlings in asynchronous broods grew slightly faster and attained slightly higher mass at 10 d of age than nestlings of the same rank in synchronous treatments. These differences, however, were not statistically significant (Wilcoxon matched-pair signed-ranks test, $T_{13} = 39$, $P > .50$; $T_{13} = 38$, $P > .50$; $T_{13} = 36$, $P > .50$; $T_{13} = 45$, $P > .50$ for growth rate and mass at 10 d of heaviest and second heaviest nestlings, respectively; Fig. 5). The penultimate, or second lightest, young in asynchronous broods grew more slowly and were lighter in mass at 10 d of age than similarly ranked young in synchronous broods (Fig. 5). Again, these findings were not statistically significant ($T_{13} = 40$, $P > .50$; $T_{13} = 40$, $P > .50$

TABLE 5. Brood size, DNM, and mean mass of nestlings at the time of brood manipulations, and subsequent patterns of divergence in mass (change in DNM) and mean gain in mass during a 6-d period after treatment began (means ± SE).*

Variable	Synchronous "parallel" broods (N = 18)	Synchronous "diverging" broods (N = 8)	Asynchronous "parallel" broods (N = 12)	Asynchronous "diverging" broods (N = 23)
Brood size†	4.5 ± 0.15	5.1 ± 0.23	4.6 ± 0.19	4.4 ± 0.18
Original DNM (g)	0.618 ± 0.068	0.463 ± 0.077	1.888 ± 0.243	1.876 ± 0.136
Change in DNM (g/d)	0.91 ± 0.014	0.254 ± 0.029	0.078 ± 0.023	0.357 ± 0.037
Final DNM (g)	1.164 ± 0.115	1.987 ± 0.225	2.357 ± 0.244	4.016 ± 0.260
Original mean‡ nestling mass (g)	5.699 ± 0.246	4.738 ± 0.339	5.962 ± 0.261	5.322 ± 0.260
Mean mass gain§ (g/d)	0.960 ± 0.035	0.949 ± 0.028	1.033 ± 0.030	0.882 ± 0.034

† $F_{3,57} = 1.89$, $P > .20$, one-way analysis of variance.
‡ $F_{3,57} = 2.41$, $P > .20$, one-way analysis of variance.
§ $F_{3,57} = 4.18$, $P > .01$, one-way analysis of variance.
* Broods are divided into four groups based on original RDNM and rates of size divergence (change in DNM of "parallel" broods is <0.18 g/d and that of "diverging" broods is >0.18 g/d).

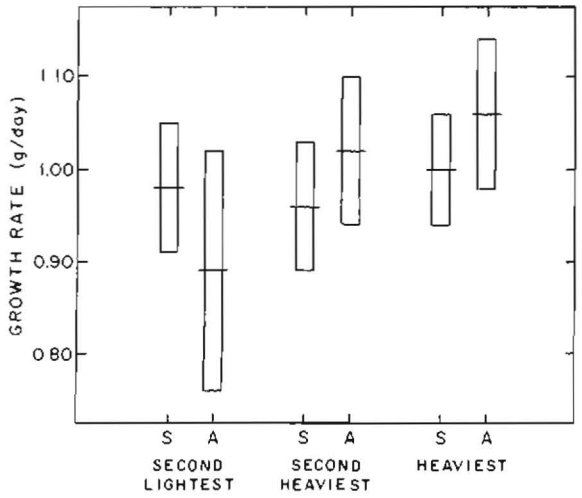

FIG. 5. Growth rates (grams per day) of the second lightest, second heaviest, and heaviest nestlings in 14 pairs of synchronous (S) and asynchronous (A) broods. Asynchronous broods in which brood reduction occurred or in which the lightest young grew more slowly ($P < .10$) than its heaviest nestmate were paired with synchronous broods that hatched within 1 d and that had no differential growth. Horizontal lines represent means and vertical bars delineate 95% CI (mean ± 2.052 SE).

for growth rate and mass at 10 d, respectively). There was, however, significantly more variation in growth rate ($F_{1,13} = 3.83$, $P < .05$) and mass at 10 d of age ($F_{1,13} = 5.82$, $P > .005$) of the second lightest young in asynchronous broods than in synchronous broods and than in all other young considered in this analysis (Fig. 5).

Implications of slow growth rates for body development

Rates of development of wing chord and tarsi were compared for 42 young with slow growth rates (grew more slowly than 1 SD below the mean growth rate of 338 young, range 0.023–0.705 g/d) and 29 nestlings with fast growth rates (> 1 SD above the mean growth rate, range 1.15–1.31 g/d). Although mean growth rates based on mass data were significantly different between these two groups (0.152 and 0.217 for slow and fast, respectively), mean growth rates of wing chord were not (0.142 for slow-growing and 0.143 for fast-growing young; Fig. 6). Tarsal development was significantly slower in nestlings with slow rates of mass gain (0.087) than in faster growing young (0.194; Fig. 6). There was little variation in the time required to grow from 10 to 90% of the wing chord asymptote (Time_{10-90}). However, there was substantial variation in Time_{10-90} in tarsal development among slow-growing individuals.

Prediction 4 and constraints on hatching asynchrony

For the following analysis, I formed four groups of nestlings along the synchrony–asynchrony continuum. To do so I subdivided nestlings in synchronous and asynchronous treatments into two further groups on the basis of whether the brood from which nestlings came fell above or below the median RDNM of that treatment (Fig. 1). The median RDNM of synchronous broods was 0.225, and in asynchronous broods equalled 0.785. I then examined growth rates and mass at 10 d of age of light, intermediate, and heavy nestlings in these four synchrony subcategories, for a total of 12 groups (Fig. 6).

Such treatment of the data could help elucidate the mode of selection responsible for observed patterns of asynchrony. For example, if growth rates alone are important in determining the degree of hatching asynchrony and stabilizing selection works to produce the normal distribution you see (Fig. 3), then the strongest selection pressures should be on the broods on the outer edges of the normal range of asynchrony.

Lightest young of synchronous broods (Fig. 6, groups 1 and 2) grew more quickly (0.896 ± 0.235 g/d) than lightest young of asynchronous broods (Fig. 6, groups 3 and 4; 0.753 ± 0.260 g/d; $t_{71} = 2.45$, $P = .017$). The basic patterns of growth rates for heavy and intermediate young were similar to each other and different from those of the lightest young. Intermediate and heavy nestlings of highly synchronous broods (groups 5 and

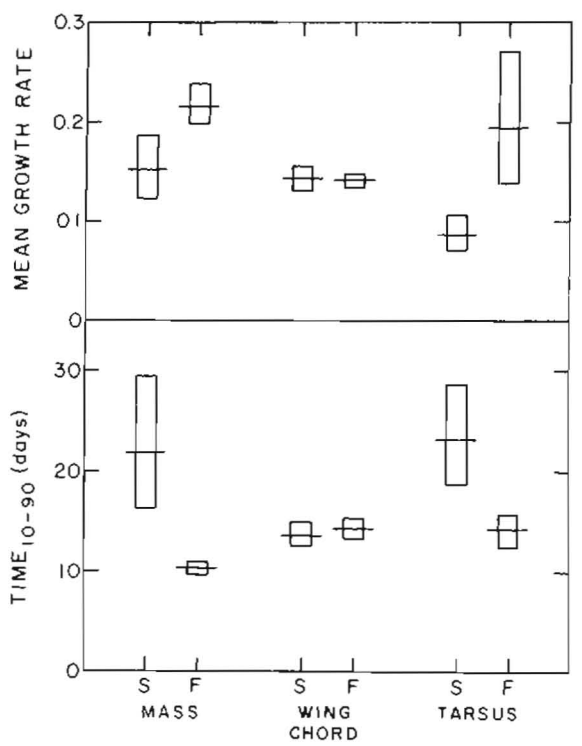

FIG. 6. Mean growth rates (of mass, wing chord length, and tarus length) and time required to grow from 10 to 90% of the asymptotic value (Time_{10-90}) of 42 slow-growing (S) and 29 fast-growing (F) young. Richard's curves (Bradley et al. 1984) were fitted to growth data.

9) and highly asynchronous broods (groups 8 and 12) grew more quickly than nestlings in less extreme broods (groups 6 and 10; groups 7 and 11; $F_{3,265} = 2.82$; $P < .05$). The same patterns were exhibited by mass at 10 d of age.

Discussion

Goldfinch broods in which the lightest nestling died of starvation were on average larger than other broods, yet there was no influence of remaining brood size on the subsequent growth rates of surviving nestlings. Although negative relationships between brood size and survival or growth of nestlings are well documented (Lack 1948, Paynter 1954, von Haartman 1954, Kuroda 1963, Perrins 1964, 1965, Klomp 1970, Askenmo 1977, Crossner 1977, Bryant 1978*a*, *b*, Cronmiller and Thompson 1980, Mock and Parker 1986), there is growing evidence from brood-enlargement experiments that, under some conditions, parents can raise more young than they attempt (Harris and Plump 1965, Loman 1980, Richter 1984).

Survivorship and growth rates of nestling goldfinches decreased throughout the breeding season. Slower growth rates late in the season may be attributed to inexperience of younger parents, or decline in food abundance and deterioration in quality of the food supply. Older goldfinches begin nesting earlier in the season and have higher fledging success than younger, less experienced parents (Middleton 1979); some parents (≈15%) produce second broods (Middleton 1979). Miller (1978) noted that goldfinches preferred immature seeds, which became less available late in the summer. Survival and growth rates decrease as breeding seasons progress in other species as well (Gibb 1950, von Balen 1973, Bryant 1978*a*, *b*, Slagsvold 1982).

In this study, cold, rainy conditions contributed to depressed growth rates of goldfinch nestlings. Adverse weather conditions lead to a conflict in allocation of parental time to brooding and foraging. When nestlings are 1–8 d old, female goldfinches contribute on average 42.7% of the food deliveries to young (S. K. Skagen, *personal observation*). If the rate of food deliveries is severely reduced because brooding requirements of young are greater, energy limitation and slower growth rates may result (Walsberg 1983). In addition, the costs of maintaining high body temperatures increase when homeothermic young are exposed to cold, rainy conditions; more energy is then used for thermoregulation and less for growth. Under adverse conditions, homeothermic young may not be able to maintain high body temperatures in the absence of a brooding parent. In September 1983, 10 young (9–10 d old) in two nests died of exposure during cold, rainy conditions. Substantial amounts of seeds were present in the false crops of these nestlings, suggesting that although food had been provided, they were unable to digest and process food fast enough to maintain homeothermy. Kenward and Sibly (1977) discuss such a "digestive bottleneck" in herbivorous birds.

Establishment of size hierarchies

Goldfinch siblings differ markedly in mass at the completion of hatching. In theory, decreasing hatchling mass with order of hatching may contribute to such size hierarchies. However, hatchling mass increased with the order of hatching in this study; this trend would reduce size differences among siblings. The size hierarchy (DNM and RDNM) at hatching was highly correlated with the hatching period; older siblings hatched on average 2 d before their youngest sibling and grew substantially during that time.

Some researchers suggest that an increase in egg mass with laying order offsets the size disadvantage to late-hatching young (Howe 1978, Slagsvold et al. 1984), yet this phenomenon is difficult to incorporate into a brood-reduction strategy. Slagsvold et al. (1984) call this a "brood survival" strategy and suggest that in species that show this trend, asynchronous hatching is not adaptive because of facilitation of brood reduction, but rather for other reasons, such as reduction of total nest failures (Hussell 1972, Clark and Wilson 1981) or spreading out peak demand (Hussell 1972). Mead and Morton (1985) doubt that such a slight decrease in size differential among siblings could compensate for age-related neurological differences that may be more important determinants of begging abilities.

Hatching periods of goldfinches increased as the season progressed. Similar trends of increasing hatching asynchrony or initial size hierarchies with time in the breeding season have been noted in other species (Gibb 1950, O'Connor 1975, Bryant 1978*b*, Mead and Morton 1985). These findings need not lend support to the brood reduction hypothesis, however. Early onset of incubation and early hatching of the oldest nestling may simply assure it more food in the face of a diminishing food supply.

Predictions 1 and 2: Does a size hierarchy at hatching facilitate differential growth of young?

Supportive evidence of predictions 1 and 2 serves to describe the positive relationship between hatching asynchrony and differential feeding of young in American Goldfinches. Growth rates of the lightest goldfinch nestlings in asynchronous broods were significantly slower than all those of all other young. These results are consistent with several other studies in which the sequence of hatching influences the survival and growth of nestlings (Ricklefs 1965, Hussell 1972, Parsons 1975, Howe 1976, 1978, Bryant 1978*a*, *b*, Strehl 1978, Zach 1982, Richter 1984, and others).

Increasing differences in the mass of the heaviest and lightest members of a brood (DNM) indicate that parents are selectively feeding the heaviest nestling at the

expense of the lightest. When the energy available for growth was low, asynchronous broods diverged more in mass than synchronous broods, both in terms of the number of broods with rapid divergence and the actual rates of divergence. These results suggest that when insufficient food is available to young, a size hierarchy does facilitate selective feeding.

Whether insufficient food reflects food scarcity in the environment or reduced food delivery rates by parents in spite of food abundance is not discernable in this study. Bryant (1978*b*) reported reduced growth rates or death of the smallest House Martin (*Delichon urbica*) nestling in broods with large size hierarchies even when food was adequate, and concluded that asynchronous hatching may be maladaptive during food abundance. This suggestion is supported by an aviary study with controlled food levels in which late-hatched Zebra Finch (*Taeniopygia guttata*) young had significantly lower survivorship than their older siblings even when food was abundant (Knight 1986). Eisner (1963) similarly reported that Bengalese Finches (*Lonchura striata*) frequently "underfed" their young in spite of ample food supplies.

Even though size hierarchies at hatching appear to facilitate selective feeding, such feeding patterns can occur even when initial size differences are small. In this study, young goldfinches in 8 of 26 synchronous broods diverged in mass so that the final difference in nestling mass was equivalent to the original size difference of asynchronous broods and to the final size difference of asynchronous "parallel" broods. Bengtsson and Ryden (1983) similarly found that size hierarchies developed out of very small initial size differences in Great Tit nestlings, and Fujioka (1985) reported the formation of dominance ranks among young in simulated synchronous broods of Cattle Egrets. Clark and Wilson (1981) argue against the brood reduction hypothesis by suggesting that even when size differences among brood members are small, hierarchies can form and the slowest growing siblings die of starvation. The rate at which this divergence occurs, however, may be important in determining how rapidly the lightest brood member is eliminated.

There are few studies that experimentally test Lack's hypothesis by reducing or exaggerating hatching synchrony. Major discrepancies in the reported findings of these studies suggest that asynchronous hatching and brood reduction may not be adaptive across all environmental conditions. Fledging success of asynchronous broods was greater than that of synchronous broods of Laughing Gulls (*Larus atricilla*) (Hahn 1981) whereas Bengtsson and Ryden (1983) found no difference in fledging success or growth rates of young between synchronous and asynchronous broods of Great Tits. Simulated synchronous broods of Cattle Egrets (*Bubulcus ibis*) (Fujioka 1985), Little Blue Herons (*Florida caerulea*) (Werschkul 1979), Fieldfares (*Turdus pilarus*), Great Tits (*Parus major*), Chaffinches (*Fringilla coelebs*), Bramblings (F. *montifringilla*) (Slagsvold 1982, 1985) fledged more young than asynchronous broods; often there were no differences between broods in the growth rates of surviving young. In this study, I also found a nonsignificant trend towards higher starvation rates in asynchronous broods.

Higher feeding rates may account for the greater fledging success of the synchronous broods cited above. Hamilton (1964) suggested that young will increase their competitive behavior when no strong hierarchy exists. Fujioka (1985) reported higher begging rates among young in synchronous broods of Cattle Egrets than in asynchronous broods. In some species, parents adjust their feeding rate according to the intensity of begging behavior of young (Henderson 1975, Bengtsson and Ryden 1983, Fujioka 1985). Parents of synchronous Cattle Egret young responded to the more intense begging by bringing more food to the nest than did parents of asynchronous young.

Husby (1986) "prevented" brood reduction from occurring in normally asynchronous broods of Magpies (*Pica pica*) by replacing nestlings after the runts died. He found no difference in growth and survival of nestlings in these experimental and control broods; however, after fledging, the survivorship of young from experimental broods was significantly lower. His study reinforces the importance of examining postfledging energy requirements and parental care before drawing firm conclusions from nestling growth and survival studies.

Interpretation of experiments involving synchrony manipulations must take into account the placement of the experimental treatments along the synchrony–asynchrony continuum characteristic of the study species. This information is often not provided by the authors. Experimental treatments that fall outside of the normal range of conditions may add no meaningful evidence towards elucidation of the evolutionary significance of asynchronous hatching.

Prediction 3: Does starvation of lightest young benefit its older nestmates?

Selective feeding that leads to differential growth of siblings does not in itself provide convincing evidence of the adaptive value of asynchronous hatching. A benefit to older nestmates in terms of higher pre- or postfledging survival or growth rates must be discernable to document such an advantage. Fledging masses and postfledging survival are positively correlated in several species (Perrins 1965, Nisbet and Drury 1972, Perrins et al. 1972, Jarvis 1974, Perrins and Moss 1975, Howe 1976, Askenmo 1977, Dhondt 1979, Garnett 1981, Drent 1984, Nur 1984; but see Hedgren 1981, Harris and Rothery 1985, Newton and Moss 1986). Prefledging masses are correlated with adult size of Zebra Finches (Knight 1986) and larger adult size correlates with breeding success in male Pied Flycatchers (*Ficedula hypoleuca*) (Lundberg et al. 1981).

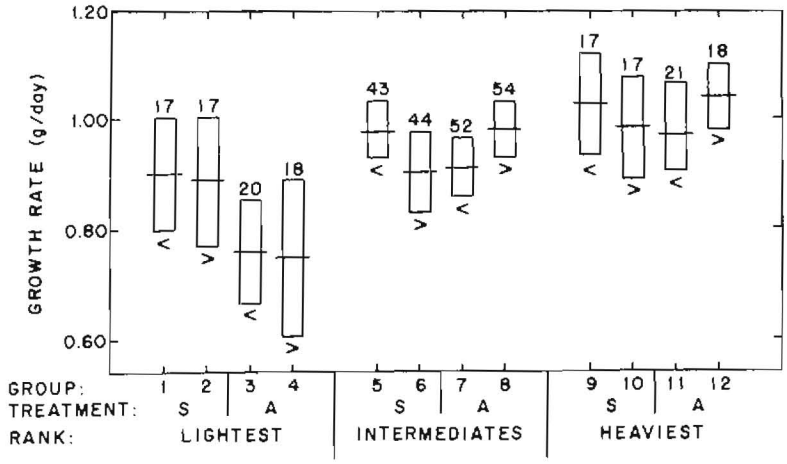

FIG. 7. Growth rates (grams per day) of nestlings in 12 groups subdivided on the basis of the degree of hatching synchrony (S, synchronous; A, asynchronous; <=RDNM < median for S and A treatment groups; >=RDNM > median for the treatment group) and the relative rank in the brood hierarchy at hatching (lightest nestling, intermediates, heaviest nestling). Horizontal lines represent means and vertical bars delineate 95% CI (mean ± 1.968 SE). Sample sizes appear above the bars. Data are included only on individuals for which growth rates could be determined; a growth rate could not be determined for the lightest member of one brood. The following comparisons are statistically significant: groups 1 and 2 differ from groups 3 and 4; groups 5, 8, 9, and 12 differ from groups 6, 7, 10, and 11. For details, see Results: Prediction 4 and Constraints on Hatching Asynchrony.

My findings do not clearly show whether there is a benefit to older young resulting from differential feeding of young. In this study, the heaviest and second heaviest nestlings in asynchronous broods that had experienced brood reduction grew more quickly than corresponding nestlings in concurrent synchronous broods. Although this trend was not statistically significant, it was in the direction predicted by Lack's hypothesis. In contrast, mortality of late-hatched Zebra Finches did not result in higher growth rates of older siblings when food was abundant, but rather indicated that under these conditions, differential feeding provides only a disadvantage (Knight 1986). Similarly, Mock (1984) recorded obligate siblicide in Great Egret (*Casmerodius albus*) chicks when abundant food was provided. These studies suggest that the mechanisms that maximize reproductive output food scarcity may in fact be counterproductive when food is abundant (Knight 1986).

Prediction 4 and constraints on hatching asynchrony in goldfinches

Growth rates alone do not explain the distribution of asynchrony (RDNM at hatching) characteristic of this population of goldfinches. Rather, patterns of growth suggest that classical disruptive selection should be working; the extreme conditions of synchrony and asynchrony led to the higher overall growth rates of nestlings than the intermediate range of asynchrony (Fig. 7). We must invoke explanations other than improved growth rates of nestlings to explain why extreme synchrony or greater asynchrony are not more common in goldfinches.

The proximate mechanism for differential feeding in small altricial species appears to operate regardless of food abundance and synchrony (Bryant 1978*a*, *b*, Knight 1986), although divergence in mass of nestmates is magnified by increasing hatching asynchrony and by food scarcity (Knight 1986). Lightest young of asynchronous broods are often at a disadvantage because of reduced growth or early mortality. This constraint would select against any asynchrony when the food supply is adequate. The intermediate range of asynchrony, although resulting in the lowest overall growth rates, would allow flexibility in response by facilitating differential feeding and growth when food is scarce, yet minimizing nestling loss when food is abundant.

Collectively, growth rates of nestlings were greatest in highly synchronous broods. Other constraints, however, may select against extreme hatching synchrony. For example, sibling rivalry and increased begging rates may reduce growth efficiency by channelling energy to more active begging rather than growth, may stimulate parents to forage at above optimal rates, or may attract predators.

In conclusion, some of the evidence presented above is consistent with the first "level" of Lack's hypothesis, i.e., that asynchronous hatching does facilitate differential feeding in goldfinches, and that late-hatched nestlings are at a disadvantage relative to their older siblings. The next "level" of the hypothesis, that this phenomenon is adaptive, is only weakly supported by the nonsignificant trend towards faster growth rates of older nestmates as a result of reduced growth rates of their lightest nestmate. I found no evidence to suggest that the primary adaptive value of hatching asynchrony in goldfinches is in promoting conditions for optimal growth in nestlings. Rather, my findings suggest that

alternative explanations for hatching asynchrony must be explored to understand more fully the adaptive value of this phenomenon in goldfinches and other temperate passerines.

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