

# AN EXPERIMENTAL TEST OF THE BROOD-REDUCTION HYPOTHESIS IN EUROPEAN STARLINGS

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**ABSTRACT.**—We manipulated hatching pattern and brood size in 102 European Starling (*Sturnus vulgaris*) broods to test the "brood reduction" hypothesis for the adaptive significance of asynchronous hatching. According to this hypothesis, asynchronous hatching in food-limited broods reduces mortality or improves the condition of nestlings in comparison with synchronous hatching.

In broods of 5 nestlings (modal clutch size was 5), overall mortality did not differ between synchronous and asynchronous (control) broods, although mortality of last-hatched nestlings in asynchronous broods was 30% higher than mortality of earlier-hatched nestlings. All last-hatched nestlings died in nests with greater asynchronous hatching than is normal for starlings. Mortality increased and fledging mass decreased in broods enlarged experimentally to 6 or 7 nestlings, which suggests food limitation in larger broods. In broods of 6 and 7 asynchronous hatching did not increase survival or fledging mass compared with synchronous broods of the same size; thus, there was no advantage to asynchronous hatching under conditions of food limitation. Similarly, brood reduction early in the nestling period did not enhance the condition of surviving nestlings, even for females forced to rear broods larger than the clutches they laid.

Most mortality of late-hatched nestlings occurred during the first 6 days after hatching. Nestlings that died during this period already diverged in mass from their surviving siblings by the age of 1 day. This early divergence in mass was probably due to asynchronous hatching, not to low food availability to the brood. Last-hatched nestlings that survived did not fledge at mass equal to their nestmates. Received 26 February 1990, accepted 7 December 1990.

IN MANY species of birds the eggs within a clutch hatch over > 1 day because parents begin incubation before the last egg is laid (reviewed by Clark and Wilson 1981, 1985). This pattern gives earlier-hatched nestlings an immediate size and motor-skill advantage over their younger siblings. Costs of asynchrony for younger nestlings include reduced growth rates and starvation (e.g. Ricklefs 1965, Howe 1976, Drummond et al. 1986) or siblicide (reviewed in Stinson 1979 and Mock 1984). Mortality of one or more nestlings (brood reduction) varies in frequency from occasional (as in some songbirds; e.g. Mead and Morton 1985, Skagen 1987) to obligate (as in some penguins and raptors; e.g. Williams 1980, Edwards and Collopy 1983).

Hypotheses for the adaptive value of asynchronous hatching stem from two perspectives. The first perspective concerns maximizing nestling survival or quality by reducing the cost of hatching failure (Stinson 1979), sibling rivalry

(Hahn 1981, Mock and Ploger 1987), or low food availability (Lack 1947). These hypotheses are all based on hatching-pattern effects on within-brood mortality. The second perspective concerns factors beyond density-dependent and asynchrony-dependent mortality, such as future reproductive success of parents (Mock and Ploger 1987), conflict of interest between parents (Slagsvold and Lifjeld 1989), or whole-brood failure, especially due to predation (Hussell 1972, Clark and Wilson 1981).

The "brood reduction" hypothesis of Lack (1947, 1954, 1968) is the most widely considered hypothesis for asynchronous hatching as a mechanism to maximize nestling quality. Lack proposed that under conditions of low food supply, the nestling mass hierarchy resulting from asynchronous hatching allows for rapid brood reduction—through starvation of the youngest nestling(s)—without adverse effects on older nestlings (Lack 1954: 152, 1968: 291). Lack stated that some species lay an extra egg that hatches asynchronously and can be reared to fledging only in above-average years (Lack 1954: 41), while other species are able to rear all young in most years and undergo brood re-

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duction only when food supply is unusually low (Lack 1954: 152). In either case the occurrence of brood reduction is regulated by food supply. Thus asynchrony is most important when brood reduction is necessary due to low food supply.

The brood-reduction hypothesis has been tested by manipulating the size differential among nestlings and examining subsequent survival and growth of nestlings. Generally, survival and size at fledging in experimentally synchronized broods have been found to be equal to or greater than in asynchronous broods in a variety of taxa (e.g. Common Cormorant, *Phalacrocorax aristotelis*, Amundsen and Stokland 1988; Cattle Egret, *Bubulcus ibis*, Fujioka 1985, Mock and Ploger 1987; Chihuahuan Raven, *Corvus cryptoleucus*, Haydock and Ligon 1986; American Goldfinch, *Carduelis tristis*, Skagen 1987). These results have been interpreted as not supporting the brood-reduction hypothesis, although food availability has rarely been manipulated or quantified. Because food supply should regulate the occurrence of brood reduction, the hypothesis cannot be discarded without considering mortality in synchronous broods when food is limited. The hypothesis would be supported, despite a cost to asynchronous broods that are not food limited, if asynchrony becomes advantageous under poor feeding conditions.

In one study in which food levels were manipulated, Skagen (1988) found differential within-brood survival due to asynchrony despite an unlimited food supply in captive Zebra Finches (*Poephila guttata*). Mortality did not differ between synchronous and asynchronous broods with reduced food availability. Skagen (1988) concluded that asynchrony was disadvantageous under normal conditions but that the reduced food treatment in the study was not sufficiently limiting to show an advantage to asynchrony.

Both hatching pattern and food supply were manipulated by Magrath (1989), who provided supplemental food to Eurasian Blackbirds (*Turdus merula*) on some territories. Fledgling survival did not differ significantly between synchronous and asynchronous broods when food was abundant, but asynchronous broods produced more surviving fledglings when feeding conditions were poor. These results provide the best support for the brood-reduction hypothesis, although Magrath's (1989) data, like those

of most other studies, suggest that asynchrony may be costly under good conditions.

Like most altricial birds (Clark and Wilson 1981, Mead and Morton 1985), European Starling (*Sturnus vulgaris*) clutches hatch over a period of approximately 24 h, with the last-laid egg hatching later than all others (Stouffer and Power 1990). Mortality of nestlings from last-laid eggs is higher than for nestlings from earlier-laid eggs, and data from a small sample of naturally synchronous broods suggest that mortality of nestlings from last-laid eggs could be avoided by synchronous hatching (Stouffer and Power 1990).

We manipulated starling broods to answer two questions about the effects of hatching pattern on nestling mortality. First, how does hatching pattern affect nestling survival and condition at fledging in a season of uncontrolled food abundance? Second, in food-limited broods, does asynchronous hatching increase survival or condition at fledging in comparison to synchronous hatching?

The first question did not test the brood-reduction hypothesis, but only quantified the cost or benefit of asynchronous hatching in normal broods. The second question provides a valid test of the brood-reduction hypothesis. Because we could not directly reduce food supply to nestlings, we reduced food availability by increasing brood size. Nestling mortality increased and condition declined as brood size increased, so this manipulation had the desired effect (see also Crossner 1977). The brood-reduction hypothesis does not require that nestlings in control (asynchronous) broods of normal size show enhanced survival or better condition in comparison with synchronously hatched broods, but it does require that asynchrony reduces the mortality or improves the condition of nestlings in food-limited broods.

#### METHODS

We studied starlings breeding in nest boxes mounted on utility poles on the Kilmer Campus of Rutgers University in Piscataway, New Jersey. The study site is a mosaic of mowed lawns, sports fields, early secondary growth, parking lots, buildings, and roads (see also Romagnano 1987).

The study population has a synchronous peak of clutch initiations in late April (Stouffer 1989, Romagnano et al. 1990). To eliminate seasonal effects, we manipulated only clutches initiated during this period (see Stouffer 1989). Clutches of 4 (26.3%) and 5

(57.6%) were most common at this time of the season in 1983–1986 (Stouffer and Power 1990). We checked each nest box at least once daily until a full clutch was laid and no new eggs had appeared for 2 days. Each day we removed fresh eggs and replaced them with artificial eggs of wood or plaster. We stored eggs at temperatures low enough to prevent development (Drent 1975; 20–25°C in 1987, 8–12°C in 1988).

We manipulated hatching patterns by replacing artificial eggs that were being incubated with real eggs that had not been incubated. We randomly assigned treatments to nest boxes. Because we tried to minimize egg storage time and we often used eggs from several females to produce experimental clutches, we were unable to control for egg size. Although variation in egg size within and among clutches has been reported for starlings, differences in mass have little effect on survival under most circumstances (Ricklefs 1984a, Greig-Smith et al. 1988). Five or six days after laying began, when incubation of artificial eggs had begun, we removed artificial eggs and added the number of eggs that were to hatch together. On the following day we added the egg that was to hatch later (if any). In the treatment with increased asynchrony (treatment 3:1:1; see below) we added another egg 2 days after we returned the first eggs. The first day that eggs hatch in a brood is referred to as day 0, as the first-hatched nestlings are 0 days old on that day. Treatment names describe the hatching pattern. For example, 3:1:1 refers to a total of 5 eggs that hatch over a 3-day period, with 3 eggs hatching on day 0, 1 egg hatching on day 1, and 1 egg hatching on day 2. In 1987 we carried out treatments 3:1:1, 4:1, and 5:0. In 1988 we repeated treatments 4:1 and 5:0 and added treatments 5:1, 6:0, 6:1, and 7:0. Treatments 3:1:1, 4:1, 5:1, and 6:1 are referred to as "asynchronous treatments"; treatments 5:0, 6:0, and 7:0 are referred to as "synchronous treatments."

We checked nests at least once daily and examined eggs for pipping beginning 11 days after we returned the first eggs. We toe-clipped nestlings uniquely within each brood and later gave nestlings USFWS bands. If eggs failed to hatch we sometimes added a nestling within the mass range of the hatched nestlings. We moved all nestlings before they were 24 h old, and in most cases they were only a few hours old. We did not replace unhatched eggs that were meant to hatch on days 1 or 2. We did not add nestlings in these cases because the period immediately after hatching was extremely important in determining survival of late-hatched nestlings (see Results).

We weighed nestlings to the nearest 0.1 g on a portable electronic balance daily on days 0–2, every other day from day 4 to 14, and every other day from day 17 through fledging. Before opening a box containing nestlings older than 14 days, we plugged the hole to prevent nestlings from jumping out of the nest. After handling the nestlings we waited for them to stop calling and to settle down into the nest before

we unplugged the hole to the box. Because nestlings were always calm before we left the box, we do not think this procedure contributed to premature fledging. Most young fledged between days 19 and 21. We considered nestlings missing from the nest on or after day 17 to have fledged; those missing earlier were considered to have died. Most nestlings that disappeared before day 17 disappeared in the first 6 days after hatching and had reduced growth compared with their siblings (see Results), so we assume that they died and were removed by parents. A nestling was considered to have died on the day it was found missing or dead. The nest boxes were built to be as inaccessible to predators as possible, and we have no reason to believe that any mortality included in these results was due to predation.

To analyze data, we used the SAS system (SAS Institute Inc. 1985). We compared frequency data with log-likelihood ratio tests (*G*-test) and report *G*-values when sample sizes were sufficient. If >25% of expected values in any frequency test were less than 5, we used Fisher's exact probability test and report only a *P*-value. To determine the asymptotic mass of nestlings (*A* g) and the rate at which the asymptote is achieved (*K* days<sup>-1</sup>), we used a nonlinear least-squares method to fit mass data to logistic equations of the form

$$M(t) = A \{1 + \exp[-K(t - i)]\}^{-1}$$

in which *M*(*t*) is the mass (g) at age *t* days and *i* is the age (days) at the inflection point of the growth curve [*M*(*i*) = 0.5*A*] (Ricklefs 1967, 1984b). We used a mixed-model nested ANOVA for analyses of growth variables, with treatment or year as main (fixed) effects and nests and nestlings within nests as random replicates (e.g. Sokal and Rohlf 1981: 289). We compared main effect means with Hochberg's GT2 method, which adjusts for unequal sample sizes (Sokal and Rohlf 1981: 245). We detail other tests as they are used.

## RESULTS

*Survival.*—In all treatments late-hatched nestlings were less likely to survive than their older siblings (Table 1). Day-1 nestlings were less likely to survive than were day-0 nestlings in treatments 4:1 and 3:1:1 in 1987 (both *P* < 0.023). Day-2 nestlings in treatment 3:1:1 never survived to fledging, surviving less often than day-0 or day-1 nestlings from treatments 3:1:1 and 4:1 combined (both *P* < 0.026). There were no differences in survival of day-0 nestlings among treatments 3:1:1, 4:1, and 5:0 (all pairwise *P* > 0.378). In 1988, results were similar for treatments 4:1 and 5:0; day-0 nestlings were equally likely to survive in both treatments (*G* = 0.342, *df* = 1, *P* = 0.558), but day-1 nestlings were less

TABLE 1. Nestling survival by year, treatment, and hatch day.

Year/treatment	Brood size	No. of broods	Hatch day	No. of nestlings	Percent fledged
1987					
3:1:1	5	8	0	24	91.7
			1	8	50.0
			2	8	0.0
Total				40	65.0
4:1	5	9	0	36	91.7
			1	9	44.4
Total				45	82.2
5:0	5	15	0	75	84.0
1988					
4:1	5	12	0	48	93.8
			1	12	66.7
Total				60	88.3
5:0	5	13	0	65	90.8
5:1	6	15	0	75	96.0
			1	15	26.7
Total				90	84.4
6:0	6	13	0	78	80.8
6:1	7	9	0	54	87.0
			1	9	22.2
Total				63	77.8
7:0	7	8	0	56	80.4
Combined					
4:1	5	21		105	85.7
5:0	5	28		140	87.1

likely to survive than were day-0 nestlings in either treatment (both  $G > 4.169$ ,  $df = 1$ ,  $P < 0.041$ ). Despite mortality of day-1 nestlings in treatment 4:1, there were no differences in overall survival between treatments 4:1 and 5:0 in either year or for both years combined (all  $G < 0.199$ ,  $df = 1$ ,  $P > 0.656$ ).

Increased brood size reduced survival in both synchronous and asynchronous broods. Mortality was higher in broods of 6 and 7 than in broods of 5 in 1988 ( $G = 4.854$ ,  $df = 1$ ,  $P = 0.028$ ). Late-hatched nestlings also followed this pattern: day-1 nestlings from treatment 4:1 survived more often than day-1 nestlings from treatments 5:1 and 6:1 ( $G = 7.252$ ,  $df = 1$ ,  $P = 0.007$ ). Although mortality increased with brood size, there were no differences in survival between synchronous and asynchronous broods of 6 or 7 (both  $G < 0.394$ ,  $df = 1$ ,  $P > 0.530$ ).

Most mortality occurred in the first few days or, to a lesser extent, in the last few days of the nestling period (Fig. 1). Considering all mortality across years and treatments, day-1 nestlings died earlier than day-0 nestlings (Kruskal-Wallis test,  $P < 0.001$ ).

*Brood reduction.*—In 1987 the modal number

of nestlings fledged matched the number of nestlings hatching on day 0 (Fig. 2). Brood reduction still occurred in 8 of 15 broods in treatment 5:0. Nests in treatment 3:1:1 were marginally more likely to undergo brood reduction than were nests in treatment 5:0 ( $P = 0.054$ ). No other treatments differed in occurrence of brood reduction in 1987 (all  $P > 0.124$ ). No treatments differed in occurrence of multiple brood reduction in 1987 (all  $P > 0.099$ ).

Results for treatments 4:1 and 5:0 were similar in 1988 (Fig. 2); occurrence of neither brood reduction nor multiple brood reduction differed between treatments 4:1 and 5:0 (both  $P > 0.434$ ). Broods of 6 and 7 (treatments 5:1, 6:0, 6:1, and 7:0 combined) were more likely to undergo brood reduction than were broods of 5 (treatments 4:1 and 5:0 combined;  $G = 17.623$ ,  $df = 1$ ,  $P < 0.001$ ). Multiple brood reduction was also more likely to occur in broods of 6 and 7 than in broods of 5 ( $P = 0.024$ ). Synchronous and asynchronous broods of 6 and 7 were equally likely to undergo brood reduction ( $P = 0.398$ ) and multiple brood reduction ( $P = 0.684$ ).

*Mass and growth.*—Variation in nestling growth during the first 4 days after hatching

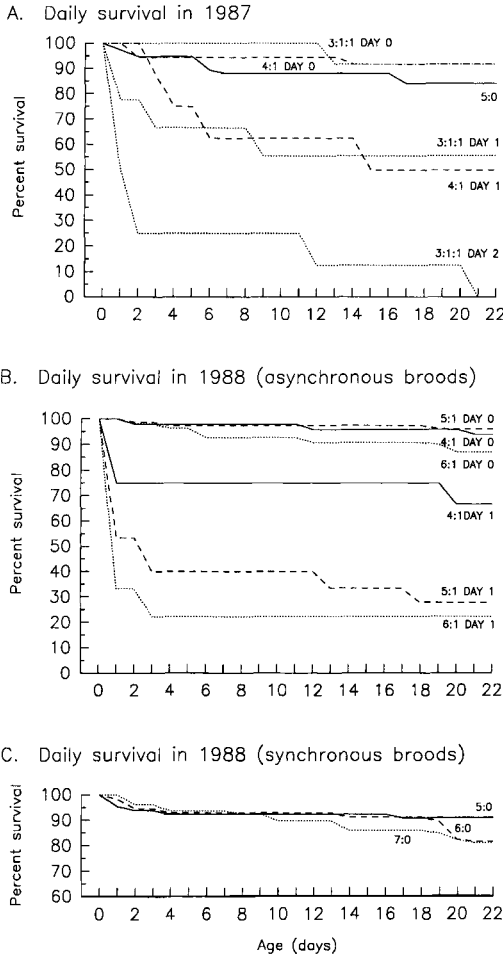


Fig. 1. Daily survival in 1987 and 1988 by treatment and day of hatching.

reveals the immediate consequences of late hatching (Fig. 3). This is the period of high mortality of late-hatched nestlings (Fig. 1). The growth of those nestlings that survived for at least 6 days after first hatch (until an age of 6 days for day-0 nestlings, 5 days for day-1 nestlings, and 4 days for day-2 nestlings) (Fig. 3: solid lines) differed from the growth of nestlings that died during the same period (Fig. 3: broken lines). Each point along the lines is based on those nestlings that survived until that day, so mortality between days reduced the sample sizes along the broken lines.

Day-1 nestlings that survived to 5 days of age diverged quickly from nestlings that died before they were 5 days old (Fig. 3b). On the day they hatched, there was no difference in mass

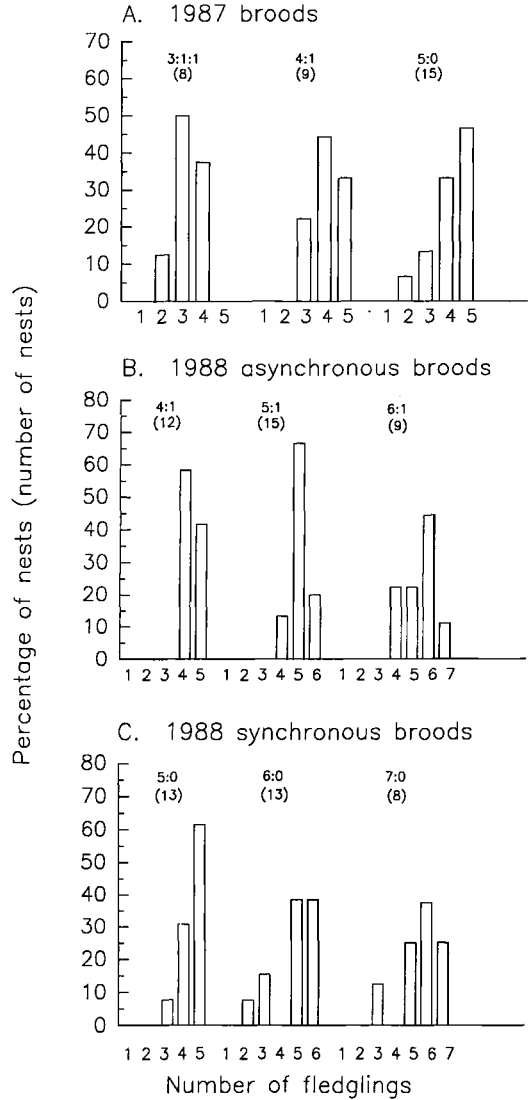


Fig. 2. Fledglings produced in each treatment.

between nestlings that subsequently survived to 5 days of age and those that did not (Kruskal-Wallis test,  $P = 0.094$ ), but by the age of 1 day there was a strongly significant difference (Kruskal-Wallis test,  $P < 0.001$ ). Similarly, at 3 days of age those nestlings that survived until 5 days of age were heavier than those that had survived for 3 days but died before 5 days (Kruskal-Wallis test,  $P = 0.005$ ).

A similar pattern of divergence occurred in the few cases of day-0 nestlings that died before they were 6 days old (7 of 237 older nestlings; Fig. 3a). Most (6 of 8) day-2 nestlings died after gaining little or no weight in the first 2 days

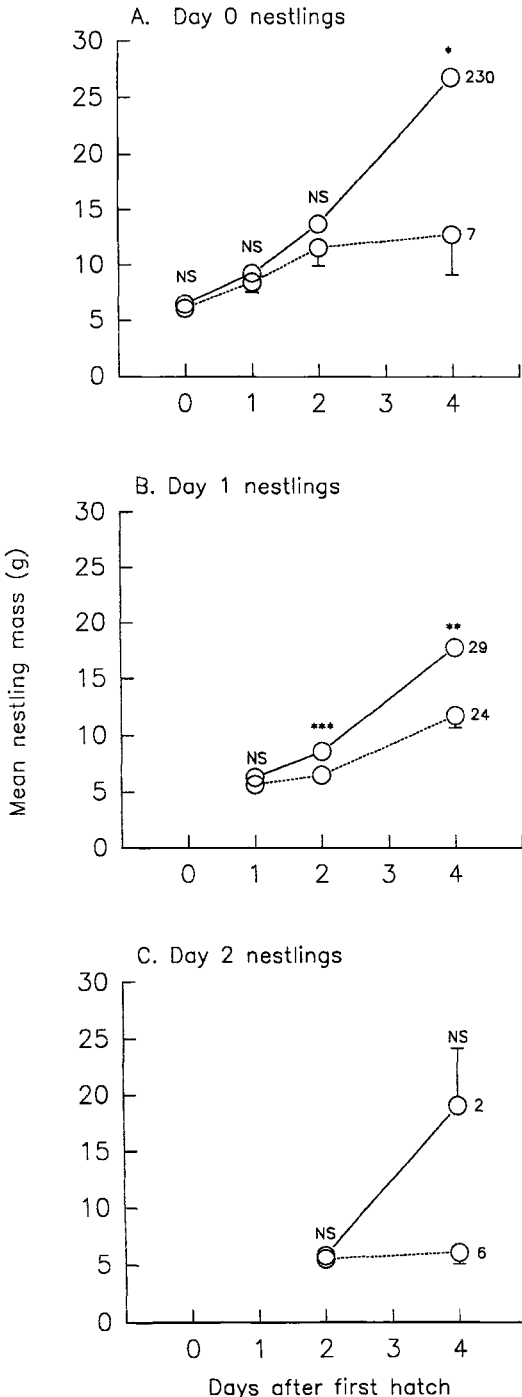


Fig. 3. Growth of nestlings that died before day 6 (dashed lines) and nestlings that survived for at least 6 days after first hatch (solid lines) in asynchronous nests. Numbers indicate the number of nestlings in each group at hatching; SE bars smaller than the symbols do not appear. Asterisks indicate significant differences (NS =  $P > 0.05$ ; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ).

after hatching, although 2 nestlings were able to gain weight and survive for at least 4 days (Fig. 3c).

Day-1 nestlings weighed less than their older siblings, even when mass was corrected for age. Considering only nestlings that survived for 6 days after first hatch (Fig. 3: solid lines), day-1 nestlings and day-0 nestlings did not differ in mass on the day they hatched (ANOVA,  $P = 0.139$ ). By the age of 1 day, however, day-0 nestlings were heavier than day-1 nestlings (ANOVA,  $P = 0.035$ ). The size advantage of older nestlings persisted in birds that survived to fledging (see below).

We examined treatment effects on nestling condition at fledging by comparing day-19 mass of nestlings that subsequently fledged (Table 2). By day 19 most nestlings had reached asymptotic mass based on analysis of growth (see below), but few had fledged.

Nestling mass differed among treatments (Table 2). In 1987, nestlings from treatment 3:1:1 were about 2-3 g heavier at day 19 than nestlings from treatments 4:1 and 5:0, but this difference was not significant. In 1988 day-19 mass declined as brood size increased, but for no brood size did nestlings in the asynchronous treatment differ in mass from the nestlings in the synchronous treatment. Nestlings from both treatments 4:1 and 5:0 were heavier on day 19 in 1988 than in 1987. Day-19 mass varied from nest to nest within each treatment (all  $P < 0.001$ ).

Day-1 nestlings that fledged weighed less than the mean mass of their older nestmates at day 19 (at an age of 18 days for day-1 nestlings and 19 days for day-0 nestlings; paired  $t$ -test,  $t = -3.5946$ ,  $P = 0.002$ ). By day 21, when they were 20 days old, surviving day-1 nestlings that had not fledged still weighed less than the mean mass of their older nestmates two days earlier ( $t = -2.664$ ,  $P = 0.020$ ).

Asymptotic mass followed a similar pattern to day-19 mass, but differences among treatments were smaller and not significant (Table 2). For all analyses asymptotic mass differed significantly among nests within treatments ( $P < 0.001$ ). Nestlings in all treatments lost mass between the age of asymptotic mass and day 19, although this decline was not significant for treatment 4:1 in 1987 (paired  $t$ -test in each treatment, all treatments except 4:1 in 1987, all  $t < -2.526$ , all  $P < 0.015$ ; treatment 4:1 in 1987,  $t = -1.801$ ,  $P = 0.080$ ). In 1987 surviving day-1 nestlings reached asymptotic masses equal to

TABLE 2. Growth rate (g/day), asymptotic mass (g) and day-19 mass (g) (all  $\bar{x} \pm SE$ ) of surviving nestlings. For each year, values followed by the same letter are not significantly different (GT2,  $P > 0.05$ ).

Year/ treatment	Brood size	No. of nestlings	Growth rate	Asymptotic mass	Day-19 mass
1987					
3:1:1	5	32	0.429 $\pm$ 0.014 A	71.84 $\pm$ 0.97 A	71.27 $\pm$ 0.99 A
4:1	5	26	0.435 $\pm$ 0.015 A	71.58 $\pm$ 1.12 A	69.40 $\pm$ 1.27 A
5:0	5	54	0.464 $\pm$ 0.008 A	69.05 $\pm$ 0.80 A	68.07 $\pm$ 0.90 A
1988					
4:1	5	53	0.480 $\pm$ 0.006 A	74.37 $\pm$ 0.79 A	73.31 $\pm$ 0.73 A
5:0	5	57	0.486 $\pm$ 0.005 A	75.20 $\pm$ 0.58 A	72.54 $\pm$ 0.65 A
6:0	6	73	0.457 $\pm$ 0.006 B	73.73 $\pm$ 0.69 A	70.35 $\pm$ 0.71 B
5:1	6	62	0.491 $\pm$ 0.005 A	72.91 $\pm$ 0.59 A	69.42 $\pm$ 0.70 B
6:1	7	44	0.481 $\pm$ 0.007 A	71.74 $\pm$ 0.95 A	68.13 $\pm$ 1.01 BC
7:0	7	37	0.499 $\pm$ 0.009 A	71.35 $\pm$ 0.74 A	66.02 $\pm$ 1.17 C

the mean of their surviving nestmates ( $t = -1.172$ ,  $P = 0.280$ ), but in 1988 surviving day-1 nestlings reached significantly lower asymptotes than their surviving nestmates ( $t = -2.798$ ,  $P = 0.015$ ).

There was no obvious pattern among growth rates as a consequence of asynchrony or brood size (Table 2). Nestlings in treatment 6:0 grew significantly more slowly than did nestlings in all other treatments in 1988, but no other treatments differed. For all treatments growth rates varied significantly among nests (all  $P < 0.001$ ). Surviving day-1 nestlings grew more slowly than the mean of their surviving nestmates in 1987 ( $t = -2.907$ ,  $P = 0.023$ ) but not in 1988 ( $t = -0.0802$ ,  $P = 0.937$ ).

*Consequences of early brood reduction.*—We examined the effects of brood reduction in the first part of the nestling period, when most day-1 nestlings died, on the condition of remaining nestlings and overall survival. For this analysis we partitioned 1988 broods by the time of brood reduction and by brood size relative to the clutch size of the female rearing the brood. We partitioned data in this way rather than by treatments for two reasons. First, some asynchronous broods did not have brood reduction in the first few days after hatching, but several synchronous broods did (Figs. 1 and 3). Second, this analysis partially controls for differences among females, since females that laid larger clutches may have been better able to rear broods of 6 and 7. Although most females laid clutches of 5 (60.0%), some females laid clutches of 3 (1.4%), 4 (18.6%), and 6 (20.0%). Unfortunately, we were unable to make equal sample sizes of all levels of enlarged and reduced, synchronous

and asynchronous broods, because females were not finished laying when we assigned treatments. Broods in which at least one nestling died before 6 days of age are referred to as EBR (early brood reduction) broods. Those broods in which no nestlings died during this period are referred to as NEBR (no early brood reduction) broods. In "normal broods" females reared broods of equal size (93.5%) or smaller (6.5%) than the clutches they laid. In "enlarged broods" females reared broods larger than the clutches they laid. Random treatment assignments stressed parents of synchronous broods more than parents of asynchronous broods, since all asynchronous broods were increased by one (50.0%) or two (50.0%) nestlings, but synchronous broods were increased by one (41.2%), two (29.4%), or three (29.4%) nestlings.

Based on the brood-reduction hypothesis, early brood reduction should enhance the condition of the remaining nestlings because less energy is spent on nestlings that do not survive until fledging. Also, efficient early brood reduction should be especially important for females forced to rear broods larger than the clutches they laid.

In contrast to the predictions of the brood-reduction hypothesis, early mortality did not improve the survival or condition of remaining nestlings (Fig. 4). Survival was significantly lower for EBR broods than for NEBR broods for both normal and enlarged broods (Fig. 4a; both  $G > 44.836$ ,  $df = 1$ ,  $P < 0.028$ ). Overall survival was higher in normal broods than in enlarged broods ( $G = 4.353$ ,  $df = 1$ ,  $P = 0.037$ ). We analyzed nestling condition using a  $2 \times 2$  mixed model ANOVA, with time of brood reduction

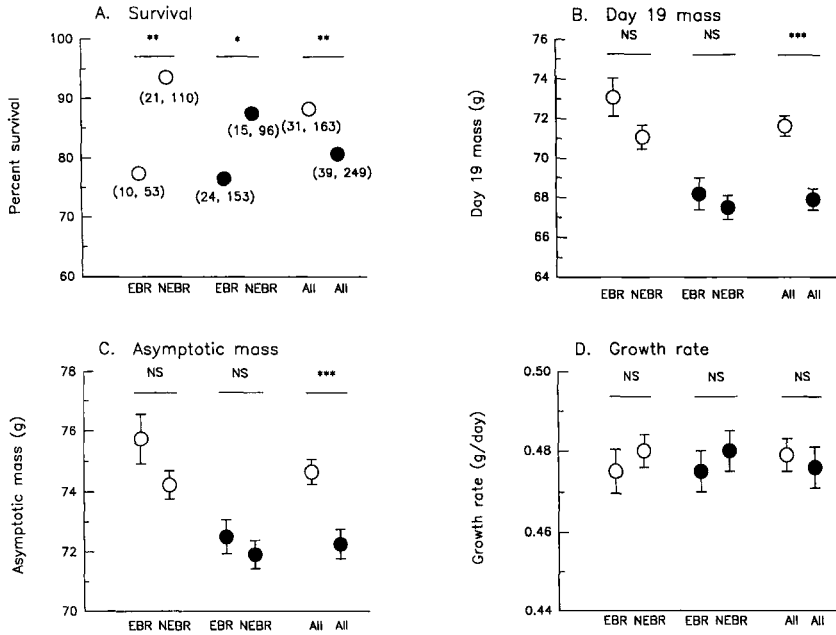


Fig. 4. Reproductive success in 1988 in normal broods (open circles) and enlarged broods (closed circles) partitioned by the timing of brood reduction (brood reduction within 6 days [EBR], no brood reduction within 6 days [NEBR], or EBR and NEBR combined [ALL]). Asterisks indicate significant differences as in Fig. 3. Numbers in parentheses indicate the number of nests, number of nestlings; SE bars are included for b, c, and d.

and brood size as main effects, and nests and nestlings within nests as replicates. As in the previous analysis of nestling condition, day-19 mass, asymptotic mass, and growth rate varied substantially from nest to nest within treatment combinations (all  $P < 0.001$ ). Day-19 mass and asymptotic mass did not differ between EBR and NEBR broods (Fig. 4: b and c; both  $P > 0.460$ ), but were reduced significantly in enlarged broods (both  $P < 0.024$ ). Neither time of brood reduction nor brood size significantly affected growth rate (Fig. 4d; both  $P > 0.351$ ). No interaction effects were significant in these analyses (all  $P > 0.388$ ).

#### DISCUSSION

*Survival in broods of 5.*—As has been found in most studies (see introduction), late-hatched nestlings in treatment 4:1 were less likely to survive than were older nestlings, although the disadvantage to these nestlings was ameliorated by experimentally synchronizing hatching. Despite high mortality of day-1 nestlings, however, there were no differences in overall survival between synchronous and asynchronous

broods of 5. We suggest that synchronous hatching would not provide a significant increase in survival in comparison to natural asynchrony, despite the advantage of synchrony for late-hatched nestlings.

Mortality of day-2 nestlings in treatment 3:1:1 clearly showed the effect of exaggerated asynchrony (Fig. 1, Table 1). The certain death of these nestlings demonstrated that, for broods of 5, nestlings hatching 2 days behind their oldest siblings could not be fledged. This means that starlings cannot begin incubation before the penultimate egg is laid if the final egg is to have a chance of producing a fledgling. Thus increasing asynchrony becomes very costly, limiting the potential for parents to fledge last-hatched nestlings even if food is plentiful. Other experimental studies have also shown reduced survival of last-hatched young in broods with exaggerated asynchrony (Slagsvold 1985, Mock and Ploger 1987, Amundsen and Stokland 1988).

*Survival in broods of 6 and 7.*—Brood reduction occurred in synchronous and asynchronous broods of 6 and 7 (Fig. 2). Because nestling mass decreased (Table 2) and brood reduction be-



came more likely in broods  $>5$  (Fig. 3), these treatments appear to have successfully reduced food availability to nestlings. Natural broods of 6 also had increased mortality and reduced nestling mass in comparison with smaller broods (Stouffer 1989, Stouffer and Power 1990). Crossner (1977) found that reduced food availability limited growth as brood size increased from 5 to 7 in his experiments with starlings at the same site. Because Crossner provided supplemental food, he demonstrated that food, not another factor (such as crowding), limited nestling growth.

*The brood-reduction hypothesis.*—The nestling hierarchy established by asynchrony did not increase the survival (Table 1) or condition (Table 2) of surviving nestlings in broods of 6 and 7. These results do not support the critical prediction of the brood-reduction hypothesis: asynchrony was not more adaptive than synchrony when food became limiting due to increased brood size.

Early brood reduction, the frequent consequence of asynchronous hatching, did little to improve the condition of remaining nestlings (Fig. 4). When parents were forced to work harder because we experimentally enlarged brood size relative to clutch size, mortality increased and nestling condition declined, regardless of the occurrence of early brood reduction. This implies that early mortality was neutral relative to the condition of remaining nestlings. We find this somewhat paradoxical. Because of the frequent inability of late-hatched nestlings to gain weight (Fig. 2), some parents were effectively rearing smaller broods from the time of hatching. If nestling condition were density-dependent, as it appears to have been (Fig. 4), this should have inevitably benefited the remaining nestlings. Even with an advantage to remaining nestlings, the brood-reduction hypothesis would not be supported unless improved condition of remaining nestlings increased parental fitness more than would survival of an additional nestling.

*Mortality and condition of late-hatched nestlings.*—Late-hatched nestlings died earlier than older nestlings (Fig. 1). Although early mortality has been considered as support for the brood-reduction hypothesis because it reduces parental investment (Lack 1968: 291, Gibbons 1987), this argument has weaknesses both for starlings and as it is generally applied. First, early mortality did not benefit the rest of the brood in

starlings. Second, reduction of investment due to mortality of a single nestling probably has little, if any, positive effect on future reproductive success of parents (Tinbergen 1987, Linden 1988, Stouffer 1989). Third, mortality of very young nestlings occurs when food demands of the brood are relatively small and appears to be due to asynchrony per se, not to food availability. Thus early nestling mortality is not an adaptive response by parents (*sensu* Williams 1966), but is a consequence of asynchronous hatching.

Late-hatched nestlings often gained little or no weight after hatching (Fig. 3), probably because they were never able to compete successfully for parental attention (Litovich 1982; see also discussion in Stouffer and Power 1990). It is less likely that too little food was available to feed the entire brood. Studies of starling feeding (Westertep 1973, Tinbergen 1981) indicate that nestling food demands do not peak until approximately 10 days after hatching, well after most mortality of late-hatched nestlings. If food were so limited that very young nestlings died, it is unlikely that the other nestlings could all survive, because their needs would soon exceed any advantage gained by loss of a single late-hatched sibling. Food limitation should therefore lead to mortality of  $>1$  nestling, and the mortality should be later in the nestling period. In contrast to this prediction, the common pattern in starlings from a variety of locations is mortality of 1 nestling soon after hatching (Dunnet 1955, Anderson 1961, Collins and de Vos 1966, Royall 1966).

Mortality of late-hatched nestlings due to starvation well before food demand peaks may be widespread, especially in species with long nestling periods (e.g. Blue-eyed Shag, *Phalacrocorax atriceps*, Shaw 1985; Common House-Martin, *Delichon urbica*, Bryant 1978; Carrion Crow, *Corvus corone*, Loman 1980). In some cases this mortality may still be related to food supply if the food brought to very young nestlings differs from that fed to older nestlings and is less common (discussed in Tinbergen 1981). However, Tinbergen (1981) found that types of food brought to nestling starlings differed little as a function of nestling age. Abundance of preferred food (leatherjacket larvae, *Tipula paludosa*) did not change significantly during first broods in England, although prey biomass increased during feeding of first broods in one year (Dunnet 1955).

Late-hatched nestlings that successfully attract parental attention soon after they hatch, probably when older nestlings are satiated, may grow enough to remain healthy. By maintaining the vigor necessary to attract their parents, they can continue to grow at a rate slightly behind their older siblings. Inability to attract parental attention in the period soon after hatching may be a risk to late-hatched nestlings in most altricial species because parents are most likely to feed bigger, more vigorous beggars (Litovich 1982; see discussion in Stamps et al. 1985). If the potential for survival of late-hatched nestlings of other species is determined as soon after hatching as it is in starlings, some studies that experimentally produced asynchronous broods by moving nestlings several days old may have underestimated the cost of asynchrony, as nestlings that were moved had already survived for several days. However, vulnerability of late-hatched nestlings soon after hatching may be ameliorated in some species. For example, Budgerigars (*Melopsittacus undulatus*) regularly hatch more asynchronously than starlings but can rear late-hatched nestlings because females feed all nestlings, regardless of begging (Stamps et al. 1985). The type of food brought to nestlings may also reduce the vulnerability of late-hatched nestlings in some species. In Great Egrets (*Casmerodius albus*), parents bring food items that can be monopolized by the most aggressive nestling. As a result, siblings fight viciously and siblicidal brood reduction is common (Mock 1985). Siblicide is less common in Great Blue Herons (*Ardea herodias*), in which parents regurgitate larger boluses that cannot be monopolized (Mock 1985).

The similarity in mortality pattern between surviving day-1 nestlings and surviving older nestlings after the first few days of the nestling period (Fig. 1) demonstrates that late-hatched nestlings that survived for the first few days reduced their mortality risk. Unfortunately for these nestlings, the cost of asynchrony was not limited to higher mortality. Surviving late-hatched nestlings fledged at lower mass than did their older nestmates. Late hatching is less costly in smaller starling broods: Ricklefs and Peters (1981) reported no difference in asymptotic mass between surviving late-hatched nestlings and their older siblings in broods of 4, a result similar to that in unmanipulated broods of 3 and 4 (Stouffer 1989).

*Nestling condition.*—Although there were no

significant differences in fledging mass as a function of asynchrony, the largest nestlings fledged from asynchronous treatments in both years (Table 2). If the contribution to parental fitness is strongly affected by fledging mass, asynchronous hatching could be favored by producing the largest fledglings. Unfortunately, our data are inadequate to quantify the optimal relationship between nestling number and quality. Small mass differences among fledglings (Table 2) may not be important in starlings, especially because nestling condition varied substantially among nests within treatments. Stromborg et al. (1988) found no relationship between mass at fledging and survival through the first few months of independence in starlings. Similar results have been reported for other species (Bryant 1975, Woolfenden 1978, DeSteven 1980). In contrast, a decline in juvenile survivorship as fledging mass declined has also been reported (e.g. Perrins 1965, Nur 1984). Krementz et al. (1989) found differential mortality among fledgling starlings as a function of mass at day 18, but it is not clear from their results if the differences were driven by low survival of a few very small birds (such as found by Nur 1984), high survival of the heaviest birds, or a more linear relationship between mass and survival.

*Hypotheses for asynchronous hatching.*—We showed that synchronous hatching did not produce the outcome predicted by the brood-reduction hypothesis. Although exaggerated asynchrony was clearly disfavored, there was very little difference in reproductive success between synchronous and asynchronous broods. Synchronous hatching is rare in starlings (Stouffer and Power 1990) and other altricial birds (Clark and Wilson 1981), so asynchrony must be maintained for reasons other than selection for adaptive brood reduction in times of food shortage.

Asynchronous hatching may allow more nestlings to fledge regardless of food supply by decreasing sibling rivalry, including siblicide (Hahn 1981, Mock and Ploger 1987), or by reducing demands on parents for food (Hussell 1972). Sibling rivalry reduction is most likely to apply to large birds that fight viciously as nestlings (e.g. herons, Mock 1984; but see Mock et al. 1987). Hussell (1972) concluded that asynchronous hatching probably cannot significantly reduce demands on parents in species with short nestling periods (e.g. open-nesting

passerines), but may apply to slowly growing species that hatch with a relatively great degree of asynchrony (e.g. House Martin; Bryant 1978, Bryant and Gardiner 1979). Given the high mortality of late-hatched nestlings in some more rapidly growing species (e.g. Red-winged Blackbird, *Agelaius phoeniceus*; Strehl 1978), reduced demands on parents may be a consequence of asynchronous hatching rather than a selective force leading to asynchrony.

Mead and Morton (1985) proposed that asynchronous hatching may not be a selected trait. This idea could be widely applied, given the lack of support other hypotheses received from many careful studies (e.g. Slagsvold 1982, 1986; Mead and Morton 1985; Skagen 1987, 1988; Amundsen and Stokland 1988; but see Magrath 1989). Further, no altricial species has been shown to regularly hatch clutches of four or more eggs synchronously, which supports Mead and Morton's (1985) contention that synchronous hatching would require substantial physiological changes that would be difficult to achieve by selection. Although synchrony is rare or nonexistent, the degree of asynchrony varies interspecifically and has clearly been modified, presumably by selection, in some highly asynchronous species. This modification may be most pronounced in the Psittacidae (e.g. Budgerigars, Stamps et al. 1985; Green-rumped Parrotlets, *Forpus passerinus*, J. R. Waltman and S. R. Beissinger pers. comm.). Slight intraspecific variation in asynchrony associated with season and habitat (e.g. Slagsvold 1986) also implies that incubation patterns can be modified, possibly by selection. Exaggerated asynchrony is costly to late-hatched nestlings in most species, so it seems unlikely that selection could favor greater asynchrony until a mechanism has evolved to insure that late-hatched nestlings receive adequate parental care (as in Budgerigars, Stamps et al. 1985).

We prevented whole-brood failure due to predation in this study, so our results do not permit direct consideration of whole-brood failure models for the adaptive significance of asynchronous hatching (Clark and Wilson 1981, Bancroft 1985). Because predation rates sometimes respond directly to observers checking nests (e.g. Howe 1979, Mead and Morton 1985), this hypothesis will remain difficult to consider in the field. Also, predation rates of hole-nesting birds using nest boxes probably do not accurately represent predation in natural cavities,

which makes an appropriate test of this model technically difficult for many well-studied species.

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