DENSITY EFFECTS ON ASYNCHRONOUS HATCHING AND BROOD REDUCTION IN EUROPEAN STARLINGS

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ABSTRACT.—We examined hatching patterns and nestling mortality in 118 European Star-
ling (*Sturnus vulgaris*) broods from 1983–1986 in central New Jersey. At most nests hatching
began on the morning of the eleventh day after clutch completion and continued 20–25
hours. Most last-laid eggs (78–93%) and 30–50% of penultimate eggs hatched on the second
day of hatching. Earlier-laid eggs hatched more synchronously. There was little variation in
hatching spread and postlaying incubation period as clutch size increased from four to six,
indicating that the amount of incubation before clutch completion increased little in larger
clutches. Mortality of nestlings from last-laid eggs accounted for 55% of all brood reduction.
Mortality of these nestlings increased from <27% in broods of three and four to >75% in
broods of five and six. Mortality of nestlings from earlier-laid eggs was less dependent on
brood size. Synchronous hatching rarely occurred naturally, but when it did occur mortality
was reduced. Mortality of nestlings from last-laid eggs in broods of three and four was
probably due to late hatching, not food shortage. *Received 24 July 1989, accepted 2 December
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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). This pattern gives
earlier-hatched nestlings an immediate size and
motor-skill advantage over their younger sib-
lings. Costs of asynchrony for younger nest-
lings include reduced growth rates and star-
vation (e.g. Ricklefs 1965, Howe 1976, Skagen
1987) or siblicide (reviewed in Stinson 1979 and
Mock 1984). Mortality of one or more nestlings
(brood reduction) varies in frequency from oc-
casional, as in some songbirds (e.g. Mead and
Morton 1985, Smith 1988) to obligate, as in some
raptors and penguins (e.g. Williams 1980, Ed-
wards and Collopy 1983).

Among species without obligate brood re-
duction (including passerines), last-hatched
nestlings are often most likely to die (Holcomb
1969, 1970; Strehl 1978; Smith 1988). This mor-
tality has been considered to be an adaptive
response, derived from asynchronous hatching,
to reduce brood size to the level dictated by the
available food supply (the *brood reduction hy-
pothesis*; Lack 1947, 1954).

Although broods larger than the mode for a
given population generally do not have in-
creased prefledging mortality (discussed in
Klomp 1970 and Richter 1984), mortality in-
creased with brood size in Great Tits (*Parus ma-
jor*; Perrins 1965) and, in one of two study years,
for Blue Tits (*P. caeruleus*; Nur 1984). This den-
sity-dependent mortality has been attributed to
the food demands of nestlings exceeding par-
ents' abilities to provide food (*sensu* Lack 1968).
Because food shortages are more likely to befall
larger broods, asynchronous hatching (and ef-
ficient brood reduction) may be especially im-
portant in larger broods (Howe 1976, Richter
1984). Alternatively, if larger clutches hatch
more asynchronously (i.e. the time required for
the clutch to hatch increases) and mortality in-
creases as the size difference within broods in-
creases, the increased mortality in larger broods
may not be due to food supply (Bryant 1975,
1978; Slagsvold 1982).

European Starling (*Sturnus vulgaris*) clutches
hatch over a period ranging from "a number of
hours" (Dunnet 1955) to "around 24 hours"
(Feare 1984: 146). The last-laid egg often hatches
later than all others (Dunnet 1944, Feare 1984:
156). Several authors reported disproportionate
mortality of nestlings from last-hatched eggs
(Dunnet 1955, Collins and de Vos 1966, Royall
1966).

We examined hatching and nestling survival in starlings to quantify the degree of hatching asynchrony and the effect of asynchronous hatching on survival. Specifically, we asked how clutch size affected hatching pattern, how hatching asynchrony affected survival, and how brood size affected survival.

METHODS

We studied starlings in nest boxes mounted on utility poles on the Kilmer Campus of Rutgers University in Piscataway, New Jersey, from 1983–1986. The study area is a mosaic of mowed lawns, sports fields, and early secondary growth as well as buildings, roads, and parking lots (see Romagnano 1987).

During each breeding season we checked nest boxes at least once daily during laying, and we weighed and individually marked eggs. *Clutch size* here refers to the number of eggs laid in a given box by the resident female. Clutch size excludes intraspecific parasite eggs added and removed before clutch initiation (Stouffer et al. 1987), and parasite eggs added during host laying (Lombardo et al. 1989, Romagnano et al. 1990). Clutches were complete when no new eggs appeared for two days after the clutch was being incubated. Eggs added after clutch completion were not part of the resident's clutch.

Beginning 10 days after clutch completion, we checked nests at least once daily and examined eggs for pipping. In 1983 we checked nests from 0900–1200 and again from 1500–1700. In 1984 most nests were checked once from 0900–1200. In 1985 nests were checked once between 1230–1600. In 1986 nests were checked between 0700–1000 and again between 1530–1730. We injected food coloring into pipped eggs so nestlings could be correctly matched with the eggs from which they hatched (Rotterman and Monnett 1984, Romagnano et al. 1989). In 1983 and 1984, we weighed newly hatched nestlings. In all years we uniquely toe-clipped nestlings within each brood.

We did not check nests after all eggs hatched (which generally took two days) until 18 days later (day 19). We refer to the day of hatching of the first egg of a clutch as day 0. On day 19 we identified surviving nestlings from toe-clip patterns. A "frontlet" placed over the entrance to each box on day 18 reduced the diameter of the entrance to the box. It permitted parents to feed nestlings but prevented young from fledging (see description in Litovich 1982 and Hoffenberg et al. 1988). We removed frontlets on day 20 and allowed young to fledge, which generally occurred by day 22. Any nestling that left the nest after frontlet removal was considered fledged.

We refer to the last-laid egg in a clutch as the *ultimate egg*, and the nestling hatching from that egg is the *ultimate nestling*. The next-to-last-laid egg and the nestling from it are referred to as the *penultimate egg* and *penultimate nestling*. Eggs laid before the penultimate are *early eggs* and hatch *early nestlings*.

Clutch initiations are highly synchronous within starling populations in the early part of the breeding season (Feare 1984: 125, Romagnano 1987). To avoid seasonal effects, we included only clutches initiated from 19 April to 1 May (during the main period of clutch initiation for the population).

We analyzed data using the SAS system (SAS Institute Inc. 1985). We compared frequencies with the log-likelihood ratio test (G-test) and report G-values when sample sizes were sufficient. We adjusted the error rate in simultaneous comparisons of data subsets following the procedure of Sokal and Rohlf (1981: 728). If more than 25% of expected values in any frequency test were greater than 5, we used Fisher's exact probability test and report only a P value. The error rate on exact probability tests cannot be adjusted when testing data subsets, resulting in a less conservative test than the log-likelihood ratio test. We detail other tests below. All tests are two-tailed.

RESULTS

Clutch initiations reached a pronounced peak early in the breeding season. Combining years, clutches were initiated in 84.9% of boxes between 19 April and 1 May. There was no decline in reproductive success during this period (number of young fledged per successful nest regressed on date of clutch initiation for each year: all $P > 0.238$) for any single year nor for all years combined. Clutches of four (26.3%), five (57.6%), and six (9.3%) were most common, combining to account for 110 of 118 clutches.

Hatching.—When we excluded eggs that were removed, abandoned, or broken by observers, 87.8% of eggs hatched in clutches of four, 90.8% in clutches of five, and 88.5% in clutches of six. Hatching success did not differ among years ($G = 4.95$; df = 3, $P = 0.176$). There was no difference in hatching success among clutch sizes of 4–6 eggs ($G = 0.57$, df = 2, $P > 0.751$, $n = 492$ eggs). Laying day had no effect on hatching in clutch sizes of 4, 5, or 6 eggs (all $G < 4.02$, df = 3, 4, 5 [clutch sizes: 4, 5, 6], all $P > 0.547$).

Most eggs pipped on the day before hatching. Repeated nest checks showed little external progress toward hatching during the day before hatching. Most newly hatched nestlings were found on the following morning (the eleventh day after clutch completion; Table 1). Hatching usually occurred within several hours of dawn; some nestlings were almost out of the shell at the morning nest check, and others still had

wet down and reddish skin, indicating that they were only 2–3 h old. These nestlings weighed less than the fresh weight of the eggs from which they hatched. By the afternoon nest check, these nestlings had dry down and yellow skin. Penultimate eggs usually hatched a few hours after early eggs, in some cases on the following morning. Clutch size had little effect on *postlaying incubation period*, defined as the time from noon of the day the last egg was laid until the first egg hatched (Table 1). The length of the postlaying incubation period did not differ among clutches of 4, 5, and 6 eggs (ANOVA, $F = 1.87$, df = 2, 63, $P = 0.163$). These data are from clutches for which we could determine the time of hatching of first- and last-laid eggs within 2 h. Nests from 1985 are excluded, because we checked nests only in the afternoon and could not reliably age the nestlings that hatched in the morning.

Ultimate eggs usually hatched 20–24 h after their early siblings. The *hatching spread* (Table 1), defined as the time between the hatching of the first- and last-laid eggs, did not differ significantly among clutches of 4, 5, and 6 eggs (ANOVA, $F = 2.60$, df = 2, 50, $P = 0.084$). Excluding the small sample of clutches of 6, hatching spread was longer in the clutches of 5 than in the clutches of 4 (ANOVA, $F = 5.13$, df = 1, 36, $P = 0.028$). Incubation period correlated negatively with hatching spread (Pearson product-moment correlation, rho = -0.59, $P < 0.001$). Sample sizes are larger for incubation period than for hatching spread because some ultimate eggs did not hatch or the time of hatching could not be determined to within 2 hours.

At seven nests, hatching took >36 h. Because we could not accurately determine the time of hatching of ultimate eggs at these nests, they were excluded from Table 1. Hatching spreads of >36 h were unrelated to clutch size (all pairwise clutch size comparisons $P > 0.227$).

We compared hatching patterns based on the dichotomous distinction of *synchronous* nestlings, which hatched on the first day of hatching for the nest, and *asynchronous* nestlings, which hatched after the first day. Ultimate eggs usually hatched asynchronously for all clutch sizes (Table 2). In clutches of 4 and 5, ultimate eggs were more likely to hatch asynchronously than were penultimate eggs, and penultimate eggs were more likely to hatch asynchronously than were early eggs (both $G > 43.15$, df = 2, $P < 0.001$). The smaller sample of clutches of 6

TABLE 1. Hatching spread and postlaying incubation period ($\bar{x} \pm$ SD). Sample sizes are in parentheses.

Clutch size	Hatching spread	Incubation period
4	20.7 ± 8.0 (13)	265.7 ± 12.6 (18)
5	24.7 ± 4.1 (35)	260.7 ± 8.3 (40)
6	22.0 ± 7.2 (5)	259.3 ± 11.3 (8)

eggs followed the same trend. Pairwise exact tests were significant between early and penultimate eggs ($P = 0.029$), and between early and ultimate eggs ($P < 0.001$). Hatching pattern did not differ between penultimate and ultimate eggs in clutches of 6 ($P = 0.077$). For clutches of 5, for which the sample was largest in all years, there was no heterogeneity among years in the proportion of eggs that hatched asynchronously ($G = 1.72$, df = 3, $P = 0.633$).

Pairwise exact tests revealed no effect of clutch size on hatching pattern for early, penultimate, or ultimate eggs (all $P > 0.107$) (Table 2). Combining all laying days, synchrony did not vary with clutch size ($G = 0.42$, df = 2, $P = 0.810$). Considering only the last 4 eggs for each clutch size, an analysis that eliminated oversampling of early eggs in larger clutches, the numerical difference in synchrony across clutch sizes remained insignificant ($G = 1.62$, df = 2, $P = 0.446$).

Survival.—Fifteen broods failed completely due to natural causes and seven broods failed due to handling of the resident female (Romagnano et al. 1989). Natural failure was independent of brood size for broods of 3–6 eggs (all pairwise $P > 0.410$). Analysis of survival excludes failed broods. *Brood size* refers to the number of eggs that hatched. Because of nonhatching, egg removal (Lombardo et al. 1989), and brood parasitism (Romagnano et al. 1990), the brood-size distribution used for analysis of survival differs from the clutch-size distribution used for analysis of hatching. For broods of 4 and 5, for which the samples were large enough in each year to test for yearly heterogeneity, there were no yearly differences in survival (both $G < 3.04$, df = 3, $P > 0.385$).

Survival differed among early, penultimate, and ultimate nestlings at all brood sizes (Table 3). At each brood size, ultimate nestlings were less likely to survive than were early nestlings (all $P < 0.043$). In broods of 3 and 5, penultimate nestlings were more likely to survive than were ultimate nestlings (both $P < 0.042$), but not in

TABLE 2. Clutch size and hatching pattern. Shown is the percentage of synchronously hatching eggs; total number of eggs is in parentheses. For each clutch size, relative laying days followed by the same letter do not differ ($P > 0.05$).

	Relative laying day				
Clutch size	Early	Penultimate	Ultimate	Combined	Last 4 eggs
4	94.2 A (52)	60.0 B (25)	21.7 C (23)	69.0 (100)	69.0 (100)
5	94.1 A (170)	73.7 B (57)	6.7 C (60)	71.8 (287)	65.1 (229)
6	86.8 A (38)	50.0 AB (8)	0.0 B (8)	68.5 (54)	57.1 (35)

broods of 4 and 6 (both $P > 0.103$). For no brood size did survival differ between early and penultimate nestlings, although this difference approached significance for broods of 5 ($P = 0.071$).

Increased brood size did not affect survival of early nestlings (Table 3; $G = 1.31$, df = 3, $P = 0.727$). Survival of penultimate nestlings declined slightly, but insignificantly, as brood size increased (all pairwise $P > 0.123$). Survival of ultimate nestlings declined markedly as brood size increased, from >64% survival in broods of 3 and 4 to <25% in broods of 5 and 6 ($G = 17.92$, df = 3, $P < 0.001$). Overall survival did not differ significantly among brood sizes, despite reduced survival of ultimate nestlings as brood size increased ($G = 7.13$, df = 3, $P = 0.068$).

We partitioned broods of 4 and 5 into the clutch sizes from which they hatched (Table 4). Considering only clutches of 5, ultimate eggs were significantly more likely to fledge in broods of 4 than in broods of 5 ($G = 7.87$, df = 1, $P =$

0.005). In broods of 4, survival of ultimate nestlings did not differ between clutch sizes ($P = 0.655$) although survival was higher for early and penultimate nestlings from clutches of 5 ($P = 0.034$).

Some ultimate and penultimate eggs hatched on the same day as their older siblings (Table 2), resulting in synchronous broods. Removal or nonhatching of ultimate eggs also produced several synchronous broods. These nests provide a comparison with the typical asynchronous broods.

Six broods of 3 nestlings hatched synchronously; 17 of the 18 (94.4%) nestlings survived (Table 5). Survival in these nests did not differ from survival in asynchronous broods of 3 ($P = 0.296$). All nestlings hatched synchronously in 8 broods of 4 nestlings. Only 1 of 32 nestlings in these synchronous broods died, significantly less than the mortality in asynchronous broods of 4 ($P = 0.040$). Two broods of 5 nestlings hatched synchronously. No nestlings died in these broods, but the sample was inadequate to

TABLE 3. Nestling survival by brood size and relative laying day. Shown is the percent survival; number of nestlings is in parentheses. For each brood size, relative laying days followed by the same letter do not differ ($P > 0.05$).

Brood size	Relative laying day			Combined
	Early	Penultimate	Ultimate	
3[a]	92.3 A (39)	100.0 A (12)	64.3 B (14)	87.7 (65)
4	90.9 A (66)	85.7 AB (28)	73.1 B (26)	85.8 (120)
5	92.9 A (85)	80.0 A (25)	24.0 B (25)	77.8 (135)
6	85.7 A (28)	71.4 AB (7)	14.3 B (7)	71.4 (42)

[a] Excludes one nestling (which fledged) for which the day of laying was uncertain.

TABLE 4. Survival in broods of 4 and 5 nestlings from clutches of 4 and 5 eggs. Shown is the percentage of surviving nestlings; total number of nestlings is in parentheses. For each column, percentages followed by the same letter do not differ.

Clutch size	Brood size	Laying day	
		Early + penultimate	Ultimate
4	4	78.8 A (33)	72.7 A (11)
5	4	94.7 B (57)	73.3 A (15)
5	5	87.5 B (88)	27.3 B (22)

TABLE 5. Survival in synchronous and asynchronous broods. For each brood size, percentages followed by the same letter do not differ ($P > 0.05$).

Brood size	Synchrony	Broods (n)	Nestlings (n)	Fledglings (n)	Percent fledged
3	Synchronous	6	18	17	94.4 A
	Asynchronous	16	48	41	85.4 A
4	Synchronous	8	32	31	96.9 A
	Asynchronous	22	88	72	81.8 B
5	Synchronous	2	10	10	100.0 A
	Asynchronous	25	125	95	76.0 A
Combined	Synchronous	16	60	58	96.7 A
	Asynchronous	63	261	208	79.7 B

show a difference ($P = 0.116$). No broods of 6 hatched synchronously. Combining broods of 3–5, survival was higher in synchronous broods ($G = 13.09$, df = 1, $P < 0.001$).

DISCUSSION

Hatching.—Several results show that females incubated for ca. 24 h before clutch completion. First, the postlaying incubation period ranged from 259–266 h (Table 1). Because starling eggs require a mean of ca. 288 h (12 days) of incubation (Ricklefs and Smeraski 1983), the first eggs to hatch must have received 22–29 h of incubation before noon of the last day of laying. Second, hatching occurred over 21–25 h (Table 1). Laying order does not affect the amount of incubation required (Ricklefs and Smeraski 1983), so the hatching spread represents the amount of incubation received by the first-laid egg before the last egg was oviposited. This relationship between postlaying incubation period and hatching spread was supported by the strong negative correlation between the two measures. Females that began incubation earlier had shorter postlaying incubation periods, but this produced a longer hatching spread. Slagsvold and Lifjeld (1989) reported a similar result for Pied Flycatchers (*Ficedula hypoleuca*).

Clutch size had little effect on hatching pattern. In clutches of 4, 5, and 6 eggs, the ultimate egg generally hatched asynchronously, although the proportion of ultimate eggs hatching asynchronously increased slightly as clutch size increased (Table 2). Postlaying incubation period did not differ among clutch sizes. Hatching spread differed only between clutches of 4 and 5, and by only 4 h (Table 1). Thus females began incubation relative to the last egg ovulated, delaying incubation in larger clutches un-

til about the time of oviposition of the penultimate egg (*sensu* Mead and Morton 1985). At all clutch sizes some females incubated before laying penultimate eggs, as these eggs sometimes hatched asynchronously (Table 2; see also Power et al. 1981). Other reports of clutch-size effects on hatching spread have shown differences of ≤4 h among the most common clutch sizes (Howe 1978, Slagsvold 1986).

Nonhatching was independent of clutch size and position in the laying sequence. Because incubation was delayed in larger clutches, the probability of hatching for earlier-laid starling eggs did not decline as clutch size increased, as has been found in several ducks (*Anas* spp.; Arnold et al. 1987).

Intraclutch egg-size variation is relatively common in birds (reviewed in Slagsvold et al. 1984). Excluding the peculiar case of penguins (Williams 1980), only in open-nesting passerines is the last egg regularly larger than the earlier eggs. This has been interpreted as an adaptation to ameliorate the disadvantage of asynchronous hatching (e.g. Howe 1976; but see Clark and Wilson 1981). Last eggs in starling clutches are generally smaller than earlier eggs regardless of clutch size (Ricklefs 1984, Greig-Smith et al. 1988, Stouffer unpubl. data), but the mass difference is due to differences in water content (not yolk provisioning), and probably has little adaptive value (Ricklefs 1984). Given the lack of variation in hatching pattern and egg size with clutch size, there is no evidence for variable patterns of parental investment as clutch size increases in starlings (*sensu* Howe 1976, 1978).

Survival.—Survival of early nestlings, which generally hatched synchronously, did not vary significantly with brood size (Table 3). Survival of penultimate nestlings also did not decline

significantly with increasing brood size. Although brood-size effects on survival of synchronously hatched nestlings have seldom been reported, Slagsvold (1982) found that brood size did not affect survival of synchronously hatched Fieldfares (*Turdus pilaris*), as did Howe (1976) for Common Grackles (*Quiscalus quiscula*).

Survival of ultimate nestlings declined markedly as brood size increased, and this mortality accounted for most brood reduction (Table 3). Results from clutches of 5 eggs suggest that ultimate-nestling mortality was due to the number of older siblings. Ultimate nestlings were 45% more likely to survive if an earlier-laid egg failed to hatch (resulting in a brood of 4) than if all eggs hatched (Table 4). Density of older nestlings also affected mortality of ultimate nestlings in experimentally produced asynchronous starling broods (Stouffer 1989).

It is less likely that density-dependent mortality of ultimate nestlings was due to relatively later hatching in larger broods, because hatching pattern varied little with clutch size. Experimentally exaggerated asynchrony increased mortality of late-hatched starlings (Stouffer 1989), Great Tits (Slagsvold 1985), and Pied Flycatchers (Slagsvold 1985), but these results were from clutches with hatching exaggerated well beyond that of even clutches of 6 in our study.

Although mortality of ultimate nestlings was density dependent, mortality of asynchronously hatched nestlings may not have been due to food limitation. Naturally synchronous broods had lower mortality than asynchronous broods (Table 5). Food limitation should have caused mortality in both groups. Also, early nestlings in broods of 5 and 6 competed with 3 or 4 same-aged siblings, but they were more likely to survive than were ultimate nestlings in broods of 3 and 4, which competed with 2 or 3 older siblings (Table 3). Food limitation should have caused higher density-dependent mortality in larger broods. Experimental synchronization also reduced mortality of ultimate nestlings in starlings (Stouffer 1989), Western Jackdaws (*Corvus monedula*, Gibbons 1987), and Fieldfares (Slagsvold 1982).

Brood size may be tightly adapted to the abilities of individual females to provide food (Högstedt 1980, Richter 1984, Pettifor et al. 1988). If this were true for starlings, mortality of ultimate nestlings in smaller broods may have been due to inferiority of females that produced smaller clutches. Females laying clutches of 4 probably were inferior, because mortality of early and penultimate nestlings was higher in broods of 4 from clutches of 4 than in broods of 4 from clutches of 5 (Table 4). Mortality of ultimate nestlings did not differ between these groups, but increased as brood size increased for females laying clutches of 5 (Table 5). Thus the fate of early and penultimate nestlings varied with female quality (as measured by clutch size), but mortality of ultimate nestlings was best predicted by brood size.

Mortality of ultimate nestlings may occur despite an adequate food supply because late-hatched nestlings (runts) are unable to compete with their older siblings for parental attention. Starling parents feed the most vigorous beggars (Litovich 1982), and the size disadvantage and less developed motor skills of runts make it unlikely that they receive any food if all nestlings are equally hungry. If older siblings are not satiated quickly, runts may become so weakened that they cannot beg effectively when older nestlings finally cease begging (Litovich 1982). Thus, despite an adequate food supply, increased density of older siblings may make it less likely that runts receive sufficient food to remain competitive. Runts hatching relatively later should be even more disadvantaged. If this is the case, a testable prediction is that runt mortality will occur soon after hatching (when begging skills of runts are least developed and they are most vulnerable to food deprivation). Alternatively, runt mortality may be due to inadequate food supply, in which case mortality should occur later, after food demands begin to stress parents (*sensu* the brood reduction hypothesis). Many runts in starling broods with manipulated asynchrony grew more slowly than their older siblings from the time of hatching, and runts often died before food became limiting to the brood. This implies an inherent disadvantage to late hatching regardless of food supply (Stouffer 1989).

Hypotheses for asynchronous hatching. —We demonstrated that asynchrony imposes a cost in the form of increased mortality of ultimate nestlings. Asynchrony-dependent mortality was reduced in synchronous broods, a result also found after experimental synchronization in other species (e.g. Shag, *Phalacrocorax aristotelis*, Amundsen and Stokland 1988; Chihuahuan Raven, *Corvus cryptoleucus*, Haydock and Ligon 1986; American Goldfinch, *Carduelis tristis*, Ska-

gen 1987). The traditional brood reduction hypothesis (Lack 1947, 1954) may still hold true, but only if food limitation would more severely affect (hypothetical) synchronous broods. This is probably not the case for starlings. Studies on experimentally enlarged starling broods showed that asynchronous hatching did not reduce mortality or improve condition of nestlings in comparison with synchronous broods when food was limiting (Stouffer 1989). Results from another experimental study showed an advantage to asynchrony under poor feeding conditions in Eurasian Blackbirds (*Turdus merula*; Magrath 1989), but it has not been shown that this advantage is sufficient to compensate for the cost of asynchrony under better conditions (see also Skagen 1988). Thus, early incubation that results in asynchronous hatching may be best explained by alternative hypotheses: as an adaptation to reduce the probability of total nest failure (Clark and Wilson 1981, Bancroft 1985), as a nonselected trait (Mead and Morton 1985), or as a consequence of parental conflict over investment (Slagsvold and Lifjeld 1989).

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