

ROLES OF EGG MASS AND INCUBATION PATTERN IN ESTABLISHMENT OF HATCHING HIERARCHIES IN THE BLACKBIRD (*TURDUS MERULA*)

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ABSTRACT.—In many species of altricial birds, eggs hatch asynchronously and the last nestling to hatch may starve to death or be killed by its older and larger siblings. Lack (1947) suggested that hatching asynchrony was adaptive because it facilitated the reduction of brood size if food was scarce after hatching, but there are many other hypotheses to explain hatching asynchrony. All adaptive hypotheses rely on the assumption that adults can control the degree of hatching asynchrony of their broods through their incubation behavior; starting incubation before laying is complete should produce asynchronous hatching. Parents potentially could enhance size hierarchies by laying a smaller egg as the last of the clutch, or reduce size hierarchies by laying a large last egg, so it has been suggested that intraclutch variation in egg mass could be adaptive by modifying hatching hierarchies. In this paper on the Blackbird (*Turdus merula*), I test the assumption that incubating females can control the hatching asynchrony of their broods, and assess the relative importance of hatching asynchrony and egg mass in the establishment of hatching hierarchies. Within clutches, the first egg tended to be the lightest and the penultimate egg the heaviest, but the last-laid egg was similar to the mean for the clutch. Incubation often started before the last egg was laid and, generally, eggs hatched in the order in which they were laid. Females started incubation earlier with respect to the last-laid egg as clutch size increased and the breeding season progressed, causing an increase in hatching asynchrony with clutch size and, in one year, laying date. Incubation apparently increased gradually through the laying sequence, rather than starting abruptly with the laying of a specific egg. Hatching asynchrony explained up to 77% of the variation in mass among siblings, while egg mass never accounted for more than 9%. Thus, hatching hierarchies primarily reflect hatching asynchrony, not egg mass. There was no effect of egg mass on the incubation period, so that egg mass did not influence hatching asynchrony. I conclude that in the Blackbird, females control the hatching asynchrony of their broods, and hatching asynchrony is far more important than egg mass in establishing hatching size hierarchies. Overall, variation in hatching asynchrony in the Blackbird is consistent with Lack's hypothesis of adaptive brood reduction, but cannot disprove other adaptive hypotheses. Received 11 March 1991, accepted 4 February 1992.

IN MANY SPECIES of altricial birds the eggs hatch asynchronously, which results in a brood of nestlings of different ages and sizes (Clark and Wilson 1981). There are many functional explanations of hatching asynchrony. Some hypotheses propose that asynchrony is merely a means by which parents can produce differences in size or age among siblings (hatching hierarchies), while others suggest that asynchrony results from selection on the timing of incubation or fledging (reviewed by Magrath 1990). All hypotheses assume that parents can control the hatching asynchrony of their broods by varying the timing of the onset of incuba-

tion. At one extreme, delaying incubation until the last egg is laid should mean that all embryos will begin development at the same time and nestlings will hatch synchronously; at the other extreme, starting incubation with the first-laid egg should result in each egg hatching in the order it was laid, at intervals equal to the intervals between laying successive eggs. If incubation starts on another egg in the laying sequence, hatching asynchrony should be intermediate. I use the term "incubation pattern" to refer to the timing of incubation during the laying period.

There are several proposed advantages of producing broods of nestlings of different sizes or ages. Lack (1947) suggested that differences in size among nestlings resulted in competitive differences, which allowed the efficient reduc-

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tion of brood size in times of food shortage. If food proved to be scarce after hatching, younger nestlings quickly died as they were out-competed by older siblings, so that the brood could be reduced to the optimal size. By contrast, if all the nestlings hatched synchronously they might be equally competitive so that food shortage could jeopardize the whole brood, rather than just the youngest nestling. There is now good evidence from many species of birds that differences in the sizes of nestlings when hatching is complete can influence the outcome of competition between siblings, although for most species it is still unclear if these differences in competitive ability result in increased parental reproductive success (Mock 1984, Magrath 1990).

Some hypotheses suggest that differences in size or age among nestlings result in greater energetic efficiency during the breeding attempt by reducing sibling rivalry (Hahn, 1981) or by spreading the peak energetic demands of individual nestlings (Hussell, 1972).

Another suite of hypotheses concerns the timing of events during the breeding cycle. For example, Clark and Wilson (1981) predicted that an equal or greater rate of predation on eggs compared to nestlings should select incubation starting with the first-laid egg because this minimizes the period when there are only eggs in the nest and means that nestlings from early-laid eggs are ready to fledge before they would have been if incubation had started later. Thus, the differences in size among nestlings may be a nonselected effect of selection for early incubation, and brood reduction might be a nonadaptive cost of early incubation.

Finally, some authors suggest that hatching asynchrony could be nonadaptive and result from physiological constraints on the timing of incubation (Mead and Morton, 1985). For a detailed discussion of hypotheses about hatching asynchrony, see Magrath (1990).

Although there have been many tests of predictions of the adaptive hypotheses, especially Lack's hypothesis of adaptive brood reduction, there have been few attempts to test the assumption on which all adaptive hypotheses rest—that parents can control the hatching asynchrony of their broods through the timing of the onset of incubation. If this assumption is incorrect, there is no need to invoke adaptation. Furthermore, even if the assumption is correct, it is necessary to know how precisely parents

can control hatching asynchrony. Clark and Wilson (1981) suggested that the incubation period of individual eggs might be sufficiently variable to produce functionally asynchronous hatching even if incubation starts after the last egg is laid. They concluded from their literature review of the few available data that "hatch spreads of 12 to 24 hours result even when incubation commences on the last egg."

The size of nestlings in a hatching hierarchy could be influenced by variation in egg mass within the clutch, as well as by hatching asynchrony. Thus, several authors have suggested that species-specific patterns of egg-mass variation are adaptive through their possible influence on hatching size hierarchies (Rydén 1978, Clark and Wilson 1981, Slagsvold et al. 1984, Hussell 1985). If brood reduction is nonadaptive, parents may lay large eggs later in the laying sequence to increase the competitive ability of late-hatching nestlings; however, if brood reduction is adaptive, parents may lay small eggs later in the sequence to reinforce competitive differences associated with hatching asynchrony (Clark and Wilson 1981, Slagsvold et al. 1984). However, Slagsvold and colleagues stressed that such hypotheses are tentative because there is insufficient information on patterns of variation in egg mass within clutches and because hatching asynchrony and egg-mass variation should be considered simultaneously. Another reason that it is necessary to consider both egg mass and hatching asynchrony is that egg mass could affect hatching asynchrony directly, if eggs of different mass have different incubation periods.

In this paper on the Blackbird (*Turdus merula*), I aim to: (1) describe the variation in egg mass within clutches; (2) assess the direct effect of egg mass on hatching asynchrony; (3) describe the pattern of incubation and hatching; (4) assess the assumption that females can control the hatching asynchrony of their broods; (5) describe variation in hatching mass hierarchies; and (6) quantify the relative importance of hatching asynchrony and egg mass in establishing hatching hierarchies.

In the Blackbird, the smallest and youngest nestling in the hatching hierarchy is more likely to die than its older and larger siblings (R. D. Magrath and A. Desrochers in prep.), and it is known that egg mass determines hatchling mass (Magrath 1992a). Furthermore, in an experimental test of Lack's hypothesis, I found

that brood reduction occurred more rapidly in asynchronous than synchronous broods, leading to higher parental reproductive success during periods of food shortage (Magrath 1989a). Thus, the Blackbird is a suitable species in which to examine the establishment of hatching hierarchies.

METHODS

Study site and population.—The study was carried out from 1985 to 1987 in the University Botanic Garden, Cambridge, England (52°12'N, 0°07'E). The Garden occupies a 16-ha site about 2 km from the city center. As well as extensive areas of lawn, there are garden beds, a rockery, a lake, and areas of woodland. About 100 pairs of Blackbirds nested in the Garden each year. The birds were used to people, and were little disturbed by routine activities including nest checks.

The Blackbird is a medium-sized thrush, subfamily Turdinae, weighing around 100 g. The sexes are very similar in mass and size, except for wing length, which is about 5% greater in males (Cramp 1988). Blackbirds lay clutches of two to five eggs in open nests. Only the female incubates, but both parents feed the nestlings (Snow 1958a). In southern England, clutches usually are laid from mid-March to late June (Snow 1955), during which a pair can raise two broods, sometimes more. Blackbird nestlings hatch asynchronously and brood reduction is common but not invariant, while depredation of eggs and nestlings is common (Snow 1958b, R. D. Magrath and A. Desrochers in prep.).

Egg mass and laying order.—When females had completed building a nest, or when the nestlings had just fledged, nests were checked each afternoon for eggs that had been laid that morning. In 1985 and 1986, each egg was numbered with a felt-tipped, waterproof marking pen on the day it was laid, to establish its laying order, and measured to the nearest 0.01 mm with dial callipers. The length of an egg can be determined uniquely; I took two measures of width, roughly at right angles, and used the mean as the breadth measure. In 1985 alone, eggs were also weighed to the nearest 0.1 g with a 10-g Pesola spring balance on the day they were laid to obtain fresh mass. Eggs were weighed only in 1985 because fresh egg mass can be predicted from an egg's dimensions and in wet, windy weather it was easier to measure than to weigh an egg. Not all nests were discovered before laying, so I could not determine the order of laying of each egg in every clutch. In 1987, eggs were not touched at laying but any eggs that had not yet hatched were marked and measured when the nest was visited during hatching.

Egg mass and hatchling size.—When the eggs in a clutch were due to hatch, I visited the nest in the morning (0500–0900) and evening (1600–2000). All

hatchlings were weighed, and marked by clipping tufts of down. There are four tufts on the head, and two on each wing, so each nestling could be identified by clipping a single tuft. All nestlings in the brood were weighed when the last nestling hatched. Nestlings were weighed to the nearest 0.1 g with a 10- or 20-g Pesola spring balance. Analyses of size hierarchies (using tibia and bill length) produced similar results to analyses of weight hierarchies, so only the latter are presented in this paper. I have reported elsewhere that egg mass explained 94% of the variation in the mass of 27 nestlings hatching at the time I visited the nest, and that the relationship was linear (Magrath 1992a).

Laying order and hatching order.—It was possible to identify the egg from which a nestling hatched if only one nestling had hatched since the last visit or if a nestling was hatching from a marked egg (sometimes a hatchling was just wearing a numbered "hat"). In other cases, if the shell had already been punctured by the bill of a nestling about to hatch, I was able to color the bill with a marking pen and so identify the hatchling on the next visit.

Age could be determined to within 0.25 days by the routine of twice-daily visits: a nestling was 0.25 ± 0.25 days old on one visit if it had not hatched on the last visit to the nest. If no other information was available, this was the estimated age, but the nestlings often could be aged more precisely. A nestling's age was known exactly if it was hatching when the nest was visited or its down was still completely wet. If the down had already dried, I estimated age from the fluffiness of the down (based on observations of nestlings of known age) and from the state of the egg on the previous visit. My estimates of age were: 0 to 20% fluffy, 0.0 days old; 20–85% fluffy, 0.1 days old; >85% fluffy, 0.25 days old (unless the nestling had already broken a large hole in the shell on the previous visit, in which case it was estimated to be 0.4 days old). Although these estimates will not be exactly correct, they are better estimates of age than the midpoint of the two visits, and I am confident that they accurately ranked the ages of nestlings within broods. My measures of hatching order followed from the estimation of age.

Incubation pattern.—I measured the incubation pattern in two ways. First, when marking eggs on the day they were laid, I recorded if the eggs were warm to the touch or if the female was incubating. A female was considered to be incubating only if she was recorded sitting on the eggs on successive visits more than about 15 min apart, because sometimes females (or even males) will cover the eggs for short periods without warming them (Snow 1958a; pers. observ.). Second, I inferred the incubation pattern from a knowledge of laying versus hatching order, and from the period between laying and hatching of marked eggs (see below).

Indices of variation in egg mass within clutches.—The

last-laid egg tends to hatch last in many species of birds, including Blackbirds, so that the mass of this egg compared with the mass of the other eggs could influence the probability that the last-hatching (most-vulnerable) nestling will survive to fledge. Therefore, I used the mass of the last-laid egg minus the mean mass of the other eggs in the clutch (the "mass difference") as an index of egg-mass variation within clutches. This is similar to the "D" value of Slagsvold et al. (1984) except that the mass of the last egg was compared with the mean mass of the other eggs, not the mean mass of the whole clutch including the last egg. This index seems more sensible biologically (a nestling only competes with its siblings, not with itself) and, in some cases, is more tractable statistically (J. J. D. Greenwood, pers. comm.).

Incubation intensity.—An association between laying order and hatching order suggests that incubation started before the last egg was laid, but it does not show whether incubation started abruptly with the laying of one egg or followed a gradual increase through the laying period. Here I derive an index which can be used to infer partial incubation based on a knowledge of the period between laying and hatching (*LHP*, in days) for eggs of known laying order.

I assume that eggs at different positions in the laying sequence in a clutch have the same rate of development for a given amount of incubation, and that they are laid at one-day intervals. Consider a clutch of three eggs where the female lays the eggs on successive days. If incubation starts abruptly when the first egg is laid, the period between laying and hatching will be the same for each egg, so they will hatch on successive days. If incubation starts when the last egg is laid, the period between laying and hatching will be two days greater for the first egg, and one day greater for the second egg, compared with the last egg, and they will hatch synchronously. If the female starts incubation abruptly 12 h before laying the last egg, or if she spends about one-half of her time incubating between laying the second and third eggs, the second egg will take one-half of a day longer to hatch than the last egg, the first egg will take a day and one-half longer, and the hatching asynchrony will be one-half of a day; the pattern will be different if incubation starts abruptly when the second egg is laid. I compute the percentage of incubation intensity (*PII*) between laying successive eggs, *i* and *i* + 1, as:

$$PII = 100[1 - (LHP_i - LHP_{i+1})]. \quad (1)$$

I define 100% incubation intensity for a given clutch size as the mean "incubation intensity" from the time the last egg is laid until the time the last nestling hatches: the intensity experienced by the last-laid egg. It is not necessarily true that 100% incubation intensity will be, in absolute terms, the same for clutches of different size. For example, females may sit for a different proportion of time on different-sized clutch-

es, or may be less able to keep eggs warm in larger clutches.

This is an ecological rather than physiological measure of "intensity," but it is appropriate when discussing hatching asynchrony, and could have advantages to a measure of incubation based only on temperature. This is because it measures, indirectly, the effect of incubation on the rate of embryo development, the crucial ecological measure. The assumption that different eggs in the laying sequence have the same rate of development for a given amount of incubation is consistent with all the data on laying order versus hatching order. Furthermore, although the embryos of some precocial species are in vocal contact late in incubation and can delay or accelerate hatching, there is no evidence of such an effect in altricial species (reviews by Freeman and Vince 1974, Drent 1975). Embryonic development in birds does not proceed at a substantial rate below about 35°C (O'Connor 1984), although some development occurs above about 25–27°C (Drent 1975). Maximum ambient temperatures at the study site only exceeded 25°C on 2 of 261 days when Blackbirds were laying eggs during the course of this study (unpubl. data), so development without incubation is unlikely to confound the results.

Statistical analyses.—Statistical analyses were performed on SPSS. They were planned by consulting SPSS guides (SPSS Inc. 1990, Norusis 1990a, b) and general statistics texts (Siegel 1956, Sokal and Rohlf 1969, Everitt 1977, Fienberg 1977, Zar 1984).

RESULTS

Egg size and mass.—The predictive equation relating egg mass to dimensions was computed by linear regression using log-transformed data:

$$M_{egg} = e^{-7.021L}L^{0.938}B^{1.904} \quad (2)$$

(*n* = 216; *r*² = 0.98), where *M*_{egg} is fresh-egg mass in grams, *L* is length in millimeters and *B* is breadth in millimeters.

Analyses of covariance revealed no difference in the slope or elevation of the regression of fresh-egg mass on egg size with laying order in the clutch (clutch size 3, *n* = 96 eggs [elevation, *F*_{2,87} = 0.26, *P* = 0.77; slope, *F*_{4,87} = 0.41, *P* = 0.80]; clutch size 4, *n* = 85 eggs [elevation, *F*_{3,73} = 0.11, *P* = 0.96; slope, *F*_{6,73} = 0.23, *P* = 0.97]; first- and last-laid eggs in all clutches, *n* = 124 eggs [elevation, *F*_{1,118} = 0.50, *P* = 0.48; slope, *F*_{2,118} = 1.01, *P* = 0.37]). All references to Blackbird "egg mass" in this paper indicate the egg mass predicted from this equation, not weighed fresh-egg mass.

Egg mass and laying order.—The mean mass of

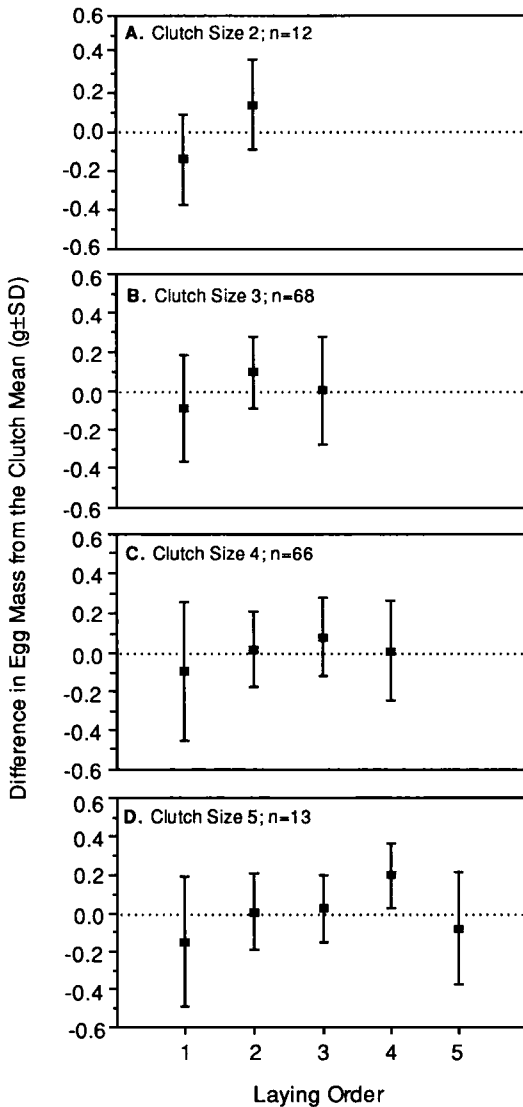


Fig. 1. Mass of each egg in clutch minus mean mass of eggs in that clutch. Effect of laying order on egg mass assessed in an ANOVA that also included clutch identity. Statistics for laying-order term were: (A) $F_{1,11} = 4.42$, $P = 0.06$; (B) $F_{2,134} = 6.34$, $P = 0.002$; (C) $F_{3,195} = 3.89$, $P = 0.01$; (D) $F_{4,48} = 2.92$, $P = 0.03$. Student-Newman-Keuls test ($P < 0.05$) showed that primary difference was between first and penultimate eggs in clutches of three to five.

772 eggs was $7.58 \pm \text{SD of } 0.68 \text{ g}$ (all eggs in the clutch measured). Egg mass changed with laying order for all clutch sizes (Fig. 1). The typical pattern for clutches of more than two eggs was that the first egg was the smallest, the penultimate egg the largest, and the last egg

close to the mean mass of eggs in the clutch. The pattern was similar in 1985 and 1986. Nonetheless, the differences of eggs from the clutch mean were small: in clutches of three and four, the common clutch sizes, the mean difference for a particular egg was never greater than 1.4%. Furthermore, more than 80% of the variation in egg mass in the population was between rather than within clutches (Magrath 1989b).

The difference in mass between the last-laid egg and the mean mass of the other eggs in the clutch ("mass difference," MD) did not differ substantially among different-sized clutches (Fig. 1; one-way ANOVA including all clutch sizes, $F_{3,155} = 2.31$, $P = 0.08$, $n = 159$; clutches of 3 and 4, $F_{1,132} = 0.03$, $P = 0.85$, $n = 134$). However, the mass difference increased through the breeding season and decreased as the mean mass of the earlier-laid eggs increased ($MD = 0.419 + [0.003\text{DATE}] - [0.207\text{MASS}]$; $F_{2,156} = 12.9$, $P < 0.001$, multiple $r^2 = 0.14$); both terms contributed significantly ($P < 0.05$) to the model. Overall, the percentage of the variance in the mass difference explained is small, about 14%, and the trends were modest: an increase of 0.1 g per month and a decrease of 0.2 g for an increase of 1.0 g in mean mass of the clutch.

Egg mass and incubation period.—If egg mass itself influences incubation period, then intra-clutch egg mass variation will affect hatching asynchrony. Therefore, it is important to examine the relationship between egg mass and incubation period. In an analysis of covariance including clutch size and incubation pattern as factors, and laying date and the mass of the last-laid egg as covariates, the partial slope of incubation period on egg mass was $0.06 \text{ days} \cdot \text{g}^{-1}$ (95% CI = -0.18 to $0.30 \text{ days} \cdot \text{g}^{-1}$; $n = 79$). Thus, egg mass did not have a clear effect on the incubation period. Females that started incubation before the last egg was laid did not lay substantially larger eggs than those that started incubation after the last egg was laid (before, $7.63 \pm \text{SD of } 0.67$, $n = 40$; after, 7.49 ± 0.50 , $n = 39$; $t = 0.97$, $df = 77$, $P = 0.34$). However, perhaps females laying large eggs were more efficient at incubating them, thus hiding any positive relationship between egg mass and incubation period. To address this problem one can look at the slope of the relationship within clutches.

If the incubation period increases with egg mass within a clutch and eggs hatch in the order laid (below), then the overall hatching asyn-

TABLE 1. Incubation pattern in relation to clutch size and date during breeding season.^a

| Variable | Initiation of incubation ^b | |
|-----------------------------------|---------------------------------------|-------|
| | Before | After |
| A. Clutch size | | |
| Small (2, 3) | 25 | 65 |
| Large (4, 5) | 60 | 28 |
| B. Date in breeding season | | |
| Early | 34 | 68 |
| Late | 51 | 25 |

^a A saturated loglinear model showed that incubation started earlier in larger clutches ($X^2 = 25.1$, $df = 1$, $P < 0.001$) and later in the season ($X^2 = 15.4$, $df = 1$, $P < 0.001$). Seasonal change was similar in different-size clutches (three-way interaction $X^2 = 0.3$, $df = 1$, $P = 0.59$). Sample sizes show number of clutches.

^b Incubation pattern dichotomized into those clutches in which incubation started before versus after last egg was laid.

chrony will be influenced by the relative size of the first- and last-laid eggs. A relatively large last-laid egg or small first-laid egg will increase the hatching asynchrony, while a small last-laid egg or large first-laid egg will reduce it. The slope of the total hatching asynchrony on the mass of last minus mass of first egg (or the smallest of the first two eggs in clutches of four and five, since incubation starts after they are laid) should estimate the effect of egg mass on incubation period. The slope was $0.04 \text{ days} \cdot \text{g}^{-1}$ (95% CI = -0.20 to $0.28 \text{ days} \cdot \text{g}^{-1}$; $n = 53$) in an analysis of covariance including clutch size, incubation pattern and laying date. These analyses show that egg mass had little or no effect on incubation period.

Incubation pattern and hatching order.—Incubation started earlier with respect to the last-laid egg as clutch size increased and the breeding season progressed (Table 1). In clutches of two and three, the modal pattern was to delay incubation until the day the last egg was laid, while in larger clutches the modal pattern was to start when the penultimate egg was laid. This change with clutch size was not simply the result of females starting incubation on a fixed egg in the laying sequence. For example, the percentage of females starting incubation on the second egg of the clutch declined from 58% to 0% as clutch size increased from two to five. Note that these data on the onset of incubation refer to records collected each afternoon; thus, they refer to the latest time that incubation could have started.

Laying order, hatching order, and incubation intensity.—Hatching order reflected laying order

TABLE 2. Hatching order in relation to laying order.^a

| Laying order ^b | Hatching order ^c | |
|---------------------------------|-----------------------------|------------|
| | Not last | Last alone |
| A. Small clutches (2, 3) | | |
| Not last | 64 | 4 |
| Last | 13 | 23 |
| B. Large clutches (4, 5) | | |
| Not last | 108 | 0 |
| Last | 3 | 31 |

^a A saturated loglinear model showed that hatching order related to laying order ($X^2 = 156.1$, $df = 1$, $P < 0.001$) and that association between laying order and hatching order was stronger in large clutches (three-way interaction $X^2 = 14.3$, $df = 1$, $P < 0.001$).

^b Egg laid last in clutch versus eggs laid earlier.

^c Birds hatching after all others ("last alone") versus those hatching earlier or hatching equal last ("not last").

in both large and small clutches, and the association between laying order and hatching order was stronger in large compared with small clutches (Table 2). Although eggs generally hatched in the order laid, in clutches of four and five the first two eggs usually hatched at the same time (21/26 and 22/26 first- and second-laid eggs hatched equal first).

The period between laying and hatching is shown for eggs of known laying order in Figure 2. These data were used to compute the mean incubation intensity on eggs through the laying sequence (Fig. 3). Three general trends are revealed: (1) incubation intensity increased through the laying period and was not 100% until the last egg was laid; (2) incubation started earlier with respect to the last egg as clutch size increased (examine the penultimate egg in clutches of three to five); and (3) incubation started later with respect to the first egg as clutch size increased (with one exception, incubation intensity on a given egg in laying sequence was lower in larger clutches). Last-laid eggs in clutches of three took longer to hatch than those in clutches of four, presumably because maximal incubation often did not start until after the last egg had been laid (the incubation periods were $13.74 \pm \text{SE of } 0.08$ days and 13.20 ± 0.15 days in clutches of three and four, respectively; $F_{1,78} = 7.09$, $P = 0.009$, $n = 82$; analysis of covariance including date of laying and egg mass).

A potential problem with these calculations of incubation intensity is that they are based on mean periods between laying and hatching. Table 1 shows that incubation starts earlier in the laying sequence late in the season and that the

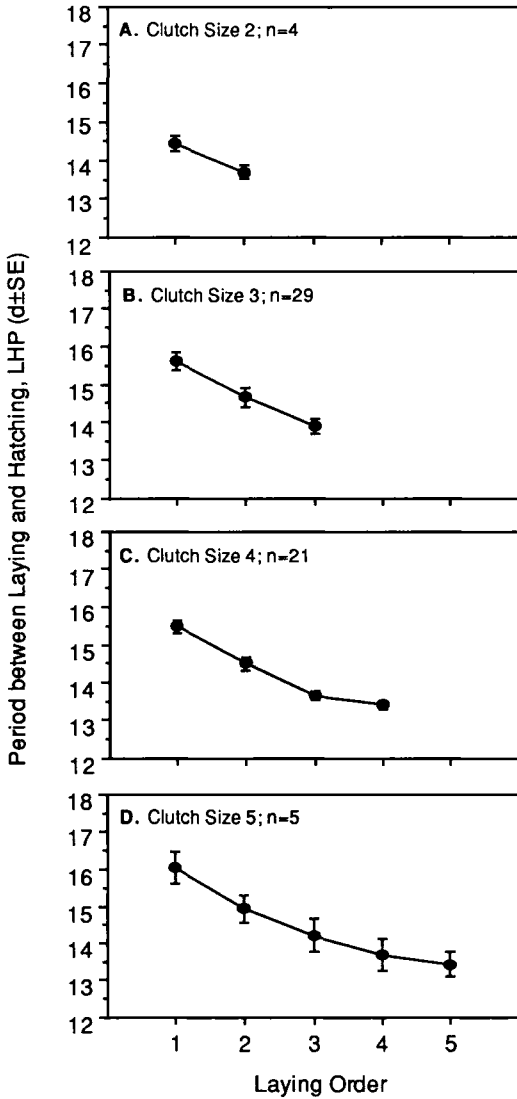


Fig. 2. Observed period between laying and hatching (LHP in text) for each egg in laying sequence. Cases included only if laying order and hatching order of each egg in clutch known. Sample sizes are number of clutches.

incubation pattern can differ between nests. Thus, "partial incubation" could be, at worst, an artefact of differences between breeding attempts. To address this problem, I examined incubation intensity in clutches in which females started incubating on the same egg in the laying sequence. The data show that incubation intensity did increase through the laying sequence (Fig. 4). It is not possible to tell from these data if the increase in incubation intensity

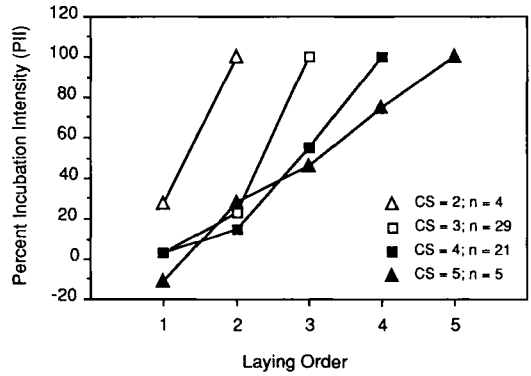


Fig. 3. Percent incubation intensity (PII) on each egg in clutches for which there was complete information (data shown in Fig. 2). See text for explanation.

was due to increasingly efficient heat transfer or to an increase in the amount of time spent incubating the eggs.

Hatching asynchrony.—Hatching asynchrony was greater in larger clutches (Table 3), and the intervals between the hatching of successive eggs increased through the hatching sequence (Table 4). In addition to a large effect of clutch

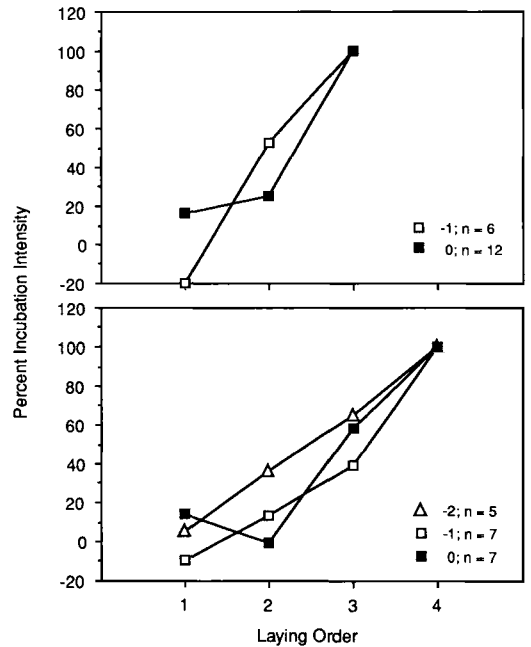


Fig. 4. Incubation intensity on each egg during the laying period in clutches of three and four. Data grouped according to egg on which female was first recorded incubating: (-2) egg before penultimate one; (-1) penultimate egg; and (0) last egg. Sample sizes are number of clutches; all incubation patterns for which $n \geq 5$ clutches are shown.

TABLE 3. Hatching asynchrony and mass differences in broods in relation to clutch size.^a $\bar{x} \pm SE$ (n).

| Clutch size | Age range ^b (days) | Mass range ^c (grams) |
|-------------|-------------------------------|---------------------------------|
| 2 | 0.41 \pm 0.15 (7) | 0.91 \pm 0.36 (7) |
| 3 | 0.57 \pm 0.04 (64) | 1.93 \pm 0.16 (72) |
| 4 | 0.86 \pm 0.05 (53) | 3.13 \pm 0.22 (65) |
| 5 | 1.31 \pm 0.17 (11) | 4.47 \pm 0.56 (10) |

^a Sample size is the number of broods.

^b Range in age between oldest and youngest nestling in brood. Cases included in analysis if all nestlings were aged to within 0.25 days, and all eggs in clutch hatched.

^c Range in mass between heaviest and lightest nestling when hatching is complete. Cases included if brood was weighed within 0.5 days of last nestling hatching, and all nestlings had hatched and were weighed.

size ($F_{1,110} = 20.4$, $P < 0.001$; only clutches of three and four were included in analysis), an analysis of covariance showed that both date and year appeared to affect hatching asynchrony. For the three years combined there was a trend for hatching asynchrony to increase through the season (hatching date within year term, $F_{3,110} = 2.58$, $P = 0.057$), although this appeared to be due entirely to a significant regression in 1986 (1985, $t = -0.14$, $P = 0.89$; 1986, $t = 2.76$, $P = 0.007$; 1987, $t = 0.31$, $P = 0.75$). Mean hatching asynchrony was lower in broods of both three and four in 1986 than in the other years (broods of three for 1985 [0.59 \pm SD of 0.29, $n = 19$], 1986 [0.53 \pm 0.32, $n = 19$], and 1987 [0.58 \pm 0.31, $n = 26$]; broods of four for 1985 [0.89 \pm 0.43, $n = 7$], 1986 [0.77 \pm 0.36, $n = 20$], and 1987 [0.93 \pm 0.36, $n = 26$]; $F_{2,110} = 3.12$, $P = 0.048$). Note that the hatching asynchrony in 1987, when eggs were not handled during laying, was similar to that in 1985, when eggs were marked and measured during laying. Thus, it appears that measuring and marking eggs

during laying did not affect hatching asynchrony.

Precision of parental control.—In clutches of four and five, the first two eggs in the laying sequence were equally likely to hatch first (above). Therefore, I used the difference in hatching times of these first two eggs to estimate the within-clutch variation in incubation periods. The first two nestlings in 17 broods of four and five hatched on average 0.13 days apart, with a mode of 0.0 days and range of 0.0 to 0.5 days. Although twice-daily visits to the nest do not allow fine resolution of hatching times in all cases, the mean should be a reasonable estimate of the true hatching interval.

As long as there is some variation in incubation periods of individual eggs, the mean hatching asynchrony will increase even if incubation never starts until the last egg is laid. This is because hatching asynchrony is a measure of range, and as sample size (clutch size) increases the chance of getting some values distant from the mean increases. Thus, it is important to know how much of the observed increase in hatching asynchrony with clutch size is due to the incubation pattern and, therefore, is under female control, and how much is due to a random increase due to increasing sample size.

I quantified the effect of random variation in hatching time on hatching asynchrony by comparing the time between first and last nestling hatching (equivalent to the "age range" in Table 3) with the difference in hatching time between the first- and last-laid eggs (order asynchrony = hatching time of the last-laid egg minus the hatching time of the first-laid egg). If a female's incubation behavior completely

TABLE 4. Mean differences ($\pm SE$) in age (days) and mass (grams) between nestlings in hatching hierarchies. Nestlings ranked by their age or mass at completion of hatching, with rank 1 being the oldest or heaviest.^a

| Brood size | n (broods) | Ranks compared ^a | | |
|--------------------------|--------------|-----------------------------|-----------------|-----------------|
| | | 1-2 | 2-3 | 3-4 |
| A. Age hierarchy | | | | |
| 3 | 64 | 0.19 \pm 0.02 | 0.38 \pm 0.04 | — |
| 4 | 53 | 0.11 \pm 0.02 | 0.22 \pm 0.03 | 0.53 \pm 0.04 |
| B. Mass hierarchy | | | | |
| 3 | 72 | 0.80 \pm 0.09 | 1.13 \pm 0.10 | — |
| 4 | 65 | 0.72 \pm 0.09 | 1.00 \pm 0.12 | 1.41 \pm 0.12 |

^a Cases included by using same criteria as those in Table 3.

^b Paired t -tests showed that there were greater differences in age between youngest nestlings and their sibs than between adjacent ranks among older nestlings in age hierarchy, in both broods of three ($t = 4.0$, $df = 63$, $P < 0.001$) and four ($t = 8.0$, $df = 52$, $P < 0.001$). Similar results found for mass hierarchies (for broods of 3, $t = 3.0$, $df = 71$, $P < 0.01$; for broods of 4, $t = 4.5$, $df = 64$, $P < 0.001$). In broods of four, mean of differences between ranks 1-2 and 2-3 used.

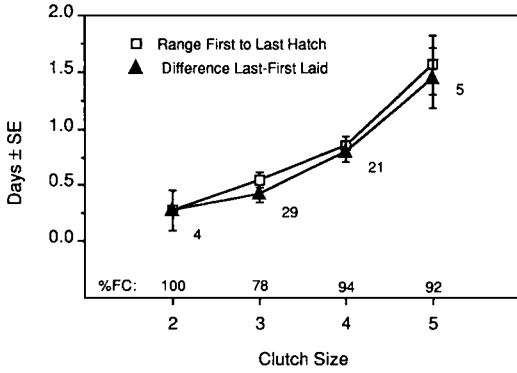


Fig. 5. Range in hatching time between first and last nestlings to hatch in a brood compared with difference in hatching time between last- and first-laid eggs in those same broods. Percentage of female control is shown at bottom of figure. See text for explanation and interpretation.

controlled the hatching asynchrony, then there would be no difference between these two measures, because the first egg would always hatch first (or equal first) and the last egg would always hatch last (or at the same time as the other eggs if incubation started on the last egg). By contrast, if random variation was the only source of variation in hatching asynchrony, total asynchrony would increase with clutch size but "order asynchrony" would be constant at zero, because the two eggs would hatch at random times about the mean. I define the "proportion of female control" over hatching asynchrony as order asynchrony divided by total asynchrony. The result of such an analysis on Blackbird asynchrony is clear. Females controlled the observed hatching asynchrony (Fig. 5), with a "proportion of control" of 78% and 94% for clutches of three and four, respectively (the clutches with adequate sample sizes). There was no sign that the curves diverged as the clutch size increased.

Establishment of hatching hierarchies.—The difference in mass between the heaviest and lightest nestlings (mass range) became greater as clutch size increased (Table 3). Lighter nestlings tended to be more different from their next-lightest siblings than were heavier nestlings (Table 4).

In addition to a large effect of clutch size ($F_{1,132} = 19.51, P < 0.001$; only clutches of three and four included in analysis of covariance), mass range became greater through the breeding season ($F_{3,132} = 3.66, P = 0.014$; hatching date

TABLE 5. Effect of hatching asynchrony and intra-clutch egg mass variation on hatching hierarchies, estimated using simple and multiple regression.^a (A) Indices of egg mass and hatching asynchrony used to predict mass of the last-hatched nestling compared with its siblings. (B) Nestling's age and mass at hatching used to predict its mass in hatching hierarchy.

| Clutch size and independent variable | R ² | R ² change |
|--------------------------------------|----------------|-----------------------|
| A. Mass of lightest nestling | | |
| 3 (n = 30 broods) | | |
| Hatching asynchrony | 0.21** | 0.24** |
| Egg weight | 0.05 | 0.08 |
| 4 (n = 21 broods) | | |
| Hatching asynchrony | 0.65** | 0.71** |
| Egg weight | 0.00 | 0.04 |
| B. Mass of each nestling | | |
| 3 (n = 135 nestlings) | | |
| Age | 0.67** | 0.71** |
| Hatchling weight | 0.05* | 0.09** |
| 4 (n = 172 nestlings) | | |
| Age | 0.76** | 0.77** |
| Hatchling weight | 0.06** | 0.08** |

*, P < 0.05; **, P < 0.01.

^a Univariate R² indicated along with change in R² when term is dropped from a regression model including both terms. Broods included if all eggs hatched and nestlings were aged to within 0.25 days. All measures of age and mass are deviances from mean for clutch or brood. Degrees of freedom in error term were reduced by number of broods because mean for each brood was used in calculating the mass-deviances of nestlings.

within-year regression) and tended to increase through the season in each year of the study. Mass range did not differ significantly between years ($F_{2,128} = 0.59, P = 0.55$).

I used two methods to assess the relative importance of hatching asynchrony and variation in egg mass within clutches in establishing hatching hierarchies. In the first type of analysis, I used indices of hatching hierarchy, within-clutch variation in egg mass, and hatching asynchrony (Table 5A). Hatching asynchrony explained a substantial amount of variation in hatching hierarchies (24% in broods of three, and 71% in broods of four), whereas egg mass explained little (8% in broods of three, and 4% in broods of four).

In the second analysis, I used differences of individual nestlings from the brood mean to estimate what proportion of the variance in their size in the hatching hierarchy is explained by age or egg mass. It was not possible to use egg mass itself because this biased the selection of broods: it was easier to identify the egg from

which a nestling hatched if the brood hatched more asynchronously. Instead, I used the mass of the nestling measured within 0.5 days of hatching to estimate the mass it would have been at 0.0 days, controlling for differences in age using the logistic growth curve (Magrath 1989b; note that the estimate of exact age of a nestling when less than 0.5 days old was based on features unrelated to its mass). Hatching mass should be a linear function of egg mass (Magrath 1992a). I transformed the age variable to make the relationship between age and mass linear, before carrying out the linear multiple regression. In the analyses both dependent and independent variables were expressed as differences about the brood means to remove the effect of variation in egg mass between clutches. The results show that the age of a nestling was a better predictor of its mass in the hatching hierarchy than was its mass at hatching: age accounted for 70% to 80% of the variance, compared with less than 10% for hatchling mass (Table 5B).

DISCUSSION

Female control of hatching asynchrony.—The evidence presented in this paper shows that females can control the hatching asynchrony of their broods through their incubation pattern, supporting the fundamental assumption on which all adaptive explanations of hatching asynchrony rest. The strong association between laying order and hatching order (Table 2) suggests that the observed hatching asynchrony was due to incubation starting before the last egg is laid, and in 48% of nests (Table 1) the female was known to have already started incubation the afternoon before the last egg was laid.

Parallel trends in incubation behavior and hatching asynchrony also suggest that females control hatching asynchrony. Females started incubation earlier with respect to the last-laid egg in larger compared with smaller clutches (Table 1). This change in incubation pattern was reflected by a stronger association between laying and hatching order in large compared with small clutches (Table 2) and an increase in hatching asynchrony as clutch size increased (Table 3). A detailed examination of the hatching patterns of marked eggs (Fig. 5) showed that the increase in hatching asynchrony with clutch size was due to the incubation pattern and not

to an increase in range associated with the greater number of eggs in larger clutches.

Even those females that started incubation before the last egg was laid did not do so until late in the laying sequence—in larger clutches the modal pattern was to start incubation with the laying of the penultimate egg. Thus, if the incubation pattern controls the pattern of hatching, the last nestling to hatch should be more different from the next-youngest nestling than the differences between adjacent ranks among older nestlings in the hatching hierarchy. The prediction is supported (Table 4A).

An earlier onset to incubation later in the breeding season (Table 1) also was reflected by a trend towards increased hatching asynchrony later in the season. However, hatching asynchrony appeared to increase only in one of the two years (1986) in which the incubation pattern was recorded. I cannot explain this anomaly.

As mentioned in the introduction, a survey of the literature suggested that hatching asynchronies of 12 to 24 h result even if incubation started with the last-laid egg (Clark and Wilson 1981). However, this is not true of Blackbirds, because even in broods of three (in which there is a mean hatching asynchrony of only 0.6 days; 14 h) there is a strong association between laying order and hatching order and 78% “female control” of hatching asynchrony (see Fig. 5 and the results section for a definition of this measure).

Overall, general trends in incubation pattern, hatching order and hatching asynchrony suggested that female Blackbirds controlled hatching asynchrony. Data on the timing of hatching of marked eggs show that they do so with a precision of under 12 h.

In studies where the eggs have been marked during laying it has been shown that eggs, especially those laid later in the sequence, often hatch in the order that they were laid (Shag, *Phalacrocorax aristotelis*, Stokland and Amundsen 1988; Blue-eyed Shag, *P. atriceps*, Shaw 1985; Herring Gull, *Larus argentatus*, Parsons 1975; Common Grackle, *Quiscalus quiscula*, Howe 1976; Tree Swallows, *Iridoprocne bicolor*, Zach 1982; Redwing, *Turdus iliacus*, Arheimer 1978; Song Thrush, *T. philomelos*, Magrath unpubl. data), and it is also common for hatching asynchrony to increase with clutch size (Magrath 1990). Patterns of hatching asynchrony in the Blackbird, therefore, are similar to many other species, so

the degree of control observed in this study may not be unusual. These results on the Blackbird suggest that the common practice of labelling as "synchronous" any brood that hatches within 24 h can be misleading, because it implies that 24 h is the minimum hatching asynchrony that is physiologically possible.

Establishment of hatching hierarchies.—Although large eggs do produce large nestlings, hatching-mass hierarchies were primarily determined by hatching asynchrony, especially in larger broods, so that patterns of variation in hatching hierarchies with brood size (Table 3) and date paralleled variation in hatching asynchrony. Furthermore, the lightest nestling was more different from the next-lightest nestling than were adjacent ranks among heavier nestlings, reflecting the pattern of hatching (Table 4). Hatching asynchrony accounted for up to 77% of the variation in mass among nestlings in the hatching hierarchy; by contrast, differences in egg mass never accounted for more than 9% (Table 5). Furthermore, these estimates of the effects of egg mass and hatching asynchrony were not confounded by a direct effect of egg mass on incubation period, as eggs of different mass did not have different incubation periods.

The proportion of the variation in mass explained by hatching asynchrony was greater in larger broods, presumably because hatching is more asynchronous in larger broods and, therefore, older nestlings have had more time to put on weight before their siblings hatch. The small effect of egg mass on hatching hierarchies reflects the small differences in egg mass associated with the laying order (Fig. 1). In particular, the last-laid egg was similar in mass to the mean for the clutch.

Is hatching asynchrony adaptive?—In an experimental study of hatching asynchrony in this population, I found that synchronous and asynchronous were equally productive when feeding conditions were good, but that asynchronous broods were more productive when food was scarce (Magrath 1989a). The results support Lack's (1947) hypothesis that hatching asynchrony facilitates adaptive brood reduction. The data reported in the current paper support an adaptive explanation because females do control the hatching asynchrony through their incubation pattern.

The gradual increase of incubation intensity through the laying sequence (Figs. 3 and 4) re-

sults in eggs usually hatching in the order laid, but without the total hatching asynchrony being too extreme. It also means that the last nestling to hatch tends to be more different from its neighbors in the hierarchy than are the older nestlings (Table 4). Thus, the youngest nestling may be at a clear competitive disadvantage. Several species have been reported to start incubation gradually, including the Blackbird (Gurr 1954, Messmer and Messmer 1956, Enemar 1958) and Redwing (Arheimer 1978, reviewed by Magrath 1990).

In this population of the Blackbird, the incidence of brood reduction is higher in larger broods (Magrath 1989b). Thus, the increase in hatching asynchrony with clutch size is consistent with Lack's (1947) hypothesis if a greater hatching asynchrony is required to facilitate brood reduction in larger broods. Perhaps in a larger brood the differences in size between nestlings have to be greater to ensure that a nestling can be singled out for starvation if feeding conditions are poor. However, this idea still needs to be tested, and Lack did not predict how much asynchrony would be required to facilitate brood reduction. Furthermore, there are other adaptive explanations of increased hatching asynchrony in larger broods. In fact, Clark and Wilson (1981) showed that more frequent starvation of late-hatching nestlings in larger broods might select for early incubation, resulting in greater hatching asynchrony. In other words, the causal relationship between hatching asynchrony and nestling starvation might be the reverse of that suggested by Lack. This is because it does not make adaptive sense to delay incubation if eggs laid later in the clutch are unlikely to produce fledglings anyway (Clark and Wilson 1981).

Seasonal patterns of variation in hatching asynchrony in Blackbirds are difficult to interpret. Earthworms, which are the single most important food source for the nestlings (Snow 1958b, pers. observ.), show a seasonal decline in availability with reduced surface activity during dry periods (Edwards and Lofty 1972). However, the availability of some alternative sources of food increases through the season (Snow 1958b, Török and Ludvig 1988). Thus, it is not clear whether there is a typical seasonal change in the predictability of the food supply. However, if hatching asynchrony facilitates brood reduction, parents might benefit by varying hatching asynchrony if at the time of laying

they have some information about the future variance in the food supply. Hatching asynchrony increased through the season in only one year, which was the only year in which there was a rapid decline in feeding conditions through the breeding season (Magrath 1989b). However, this increase of hatching asynchrony through the season in 1986 occurred because early clutches hatched unusually synchronously. The temperature in early April 1986 was also low compared with the other years and the first-clutch laying peak coincided with a week in which the mean temperature dropped below 5°C (Magrath 1989b), the threshold temperature for the onset of laying in Blackbirds (Myres 1955). Low temperature might, therefore, have been the cue or the constraint which resulted in the more synchronous hatching in early 1986 and the seasonal pattern of increase. It seems most parsimonious to suggest that the cold weather meant that females could not afford to lay eggs and incubate at the same time, therefore delaying incubation and causing more synchronous hatching.

Slagsvold (1986) and Slagsvold and Lifjeld (1989) also argued that the greater hatching synchrony found during colder weather and in marginal habitats in the Pied Flycatcher (*Ficedula hypoleuca*) probably resulted from energetic constraints during laying. Similarly, Enemar and Arheimer (1989) found that passerines nesting in Swedish Lapland delayed incubation in an unusually cold, wet year.

Finally, Blackbird females do not always start incubating on a specific egg in the laying sequence; the incubation pattern can differ between nests, and starts earlier in larger clutches and later in the season. This suggests that the incubation pattern could respond to selection and is not under strong phylogenetic constraint, as argued by Mead and Morton (1985).

I conclude that the data on incubation patterns and hatching asynchrony support the assumption that females can control the hatching asynchrony of their broods, and that the natural variation in hatching asynchrony is consistent with Lack's hypothesis of adaptive brood reduction. Thus, the data are consistent with the conclusion of an experimental study that hatching asynchrony can facilitate adaptive brood reduction (Magrath 1989a). However, the data presented in this paper cannot rule out other adaptive explanations.

Is intraclutch egg mass variation adaptive?—There

was no evidence that intraclutch variation was an adaptation to enhance or reduce the probability of brood reduction. Variation in egg mass had little effect on hatching size hierarchies. On average the last-laid egg was the same as the clutch mean; there was no difference in the relative size of the last egg in clutches of different size. The seasonal increase in the *MD* (the difference in mass between the last-laid egg and the mean of the other eggs) of 0.1 g per month seems too small to have any important effect on hatching hierarchies. In broods of three the lightest nestling was 1.9 g less than the heaviest nestling and in broods of four it was 3.1 g lighter (Table 3). The observed decrease in *MD* of 0.2 g for an increase of 1 g in the mean mass of eggs laid before the last egg also would not have a large effect on hatching hierarchies.

Authors of other studies in which the relative importance of egg mass and hatching asynchrony was quantified also have concluded that egg mass is unimportant compared to hatching asynchrony (Bryant 1978, Bancroft 1984, Stokland and Amundsen 1988; reviewed by Magrath 1990). For example, Bancroft found that the small last-laid egg of the Boat-tailed Grackle (*Quiscalus major*) contributed less than 0.3 g (6%) to the mean 5-g range in mass in the hatching hierarchy in a brood of three.

Rather than being adaptive through its effect of hatching hierarchies, variation in egg mass within clutches might simply reflect energetic constraints during laying, as Järvinen and Ylimaunu (1986), Ojanen et al. (1981), Järvinen and Pyl (1989), and Slagsvold and Lifjeld (1989) have suggested. In the Botanic Garden population of the Blackbird, I found that the mean egg mass increased through the season, and that this was probably due to a decreasing cost of egg production as temperatures rose (Magrath 1992b). I also found that the last-laid egg was the one most vulnerable to variation in air temperature during the prelaying period, and suggested that interspecific differences in the mass of the last-laid egg compared with earlier eggs (*MD*) might reflect a strategy to avoid producing unviable last-laid eggs. The last-laid egg might have to be relatively larger in species in which the variance is greater. However, I cannot think of an adaptive explanation for the slight increase in egg mass from the first-laid to penultimate egg in the clutch.

I conclude that variation in egg mass within clutches does not have an important effect on

hatching hierarchies. Egg mass variation might reflect primarily the energetic constraints faced by females.

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