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DEVELOPMENT AND MAINTENANCE OF NESTLING SIZE HIERARCHIES IN THE EUROPEAN STARLING

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ABSTRACT.—In this paper we show that nestling mass hierarchies in the European Starling (*Sturnus vulgaris*) are due to asynchronous hatching. The parents may, by starting to incubate the day the penultimate egg is laid, or earlier, affect the degree of hatching asynchrony and thereby the nestling weight hierarchy. Intra-clutch variation in egg size had no effect on nestling weight hierarchies, explaining only 0.4% of the variation in nestling mass at two days of age. Nestlings kept their relative size to siblings throughout a substantial part of the nestling period. Furthermore, the degree of variation in mass at two days of age affected the variation in mass at least until nine days. This relationship was stronger in larger broods. *Received 13 Sept. 1993, accepted 30 Jan. 1994.*

For most or all bird species, the conditions for raising young are unpredictable. If the nestlings within a brood compete with each other for food, selective brood reduction might be beneficial for the parents when there is not enough food for all nestlings to survive (Lack 1947). Hence, in unpredictable environments, it might be beneficial for parents to create a size hierarchy among nestlings to facilitate early brood reduction when food is scarce. There are at least two ways for parents to create nestling size hierarchies. First, in most bird species incubation starts before the last egg is laid, with the result that one or several nestlings hatch after their siblings (Clark and Wilson 1985). Second, the variation in egg size with laying sequence might contribute to nestling size hierarchies if, for example, late laid eggs are smaller (Rydén 1978, Slagsvold et al. 1984). However, it is not well known how hatching asynchrony and egg size variation contribute to nestling size hierarchies (Magrath 1990). For example, nestling size hierarchies may develop soon after hatching, even when hatching is synchronous (Clark and Wilson 1981), and egg size variation might be too small to contribute to variation in nestling mass (Magrath 1990). Furthermore, if the feeding rates of individual nestlings are under parental control, size hierarchies may not have any important effect on the growth rate and mortality risk of nestlings.

The aim of this paper is to show how nestling size hierarchies in the European Starling (*Sturnus vulgaris*) are affected by natural variation in hatching asynchrony and egg size and to assess if early size hierarchies are maintained during the early nestling period.

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METHODS

We studied starlings from March to June 1992, in the Revinge area (55°42′N, 13°28′E), 20 km ESE of Lund, in southern Sweden. The area is characterized by open pastures grazed by cattle, interrupted by shrub and small forests. Starlings bred in 11 colonies containing 12–15 nestboxes of similar size. During the egg laying period, nestboxes were visited once daily between 10:00 and 13:00 h. Eggs were marked individually with an indelible marker the day of laying and weighed to the nearest 0.05 g using a 10-g Pesola spring balance mounted in a glass-tube (as a wind-shield). If two new eggs were discovered in a nest on the same day, one of them was considered to have been laid by a parasite female (Feare 1984). In this study, the parasite's egg always was easy to recognize, since it differed from the other eggs in size, color, and/or shape (see Stouffer et al. 1987, Evans 1988). Eggs of parasites were transferred to other nests not included in this study. Eggs occasionally were thrown out during laying, presumably by a parasitic female (Lombardo et al. 1989). In five cases, one egg was missing or destroyed and replaced with another unincubated egg of similar mass. The majority of the nests included in this study were subject to an experimental study on the effect of egg size on fitness (Smith et al., in press). The experiment consisted of switching similar-sized clutches completed on the same day. Switching occurred the day after clutch completion. Since the purpose of this study was to evaluate how variation in egg size and hatching spread affected nestling size hierarchies, rather than the effect of parental attributes, we pooled data from the experimental and control broods. This study included a total of 31 clutches from the experiment, six sham-manipulated clutches (eggs temporarily removed) and four control broods.

Nests were visited daily between 07:00 and 17:00 h. Newly hatched chicks were weighed and marked with a segment of a drinking straw around their tarsi (Harper and Neill 1990). The age of hatchlings was estimated using a method described by Stouffer and Power (1990). Hatchlings were estimated to be, on average, 1.5 h old if they had red skin and wet down, and on average, 4.5 h old if they had red skin and dry down, and older if their skin had turned yellow. Nestlings were weighed when they were 1, 2, 3, 4, 5, 6, 7, 9, 11, and 14 days old (day 0 being the day of hatching). Nestboxes were visited later in order to determine if any nestlings failed to fledge.

Statistics were performed with SYSTAT (Wilkinson 1990). We tested for interactions in all multivariate analyses but excluded them unless significant. For cases where we had ordered expectations, isotonic regression was used (Gaines and Rice 1990).

RESULTS

The degree of size hierarchy among nestlings was affected by the nestlings' spread in hatching time. For this analysis we only included nestlings whose hatching time was well known (i.e., encountered when still red) and only broods where this was known for at least four nestlings. This left 15 nests in which, on average, 4.4 out of 5.5 nestlings had known hatching times. In only one case was the hatching time of the last-hatched young not known. Since all nestlings were not hatched until day 2, we used mass day 2 to calculate the dependent variable. Following Harper et al. (1993), we used the coefficient of variation as the measure of the hierarchy. Variation in mass at day 2 was positively related to the variation in hatching time (Fig. 1). When estimating the effect of the variation in egg mass on nestling size hierarchies, we used only clutches where we

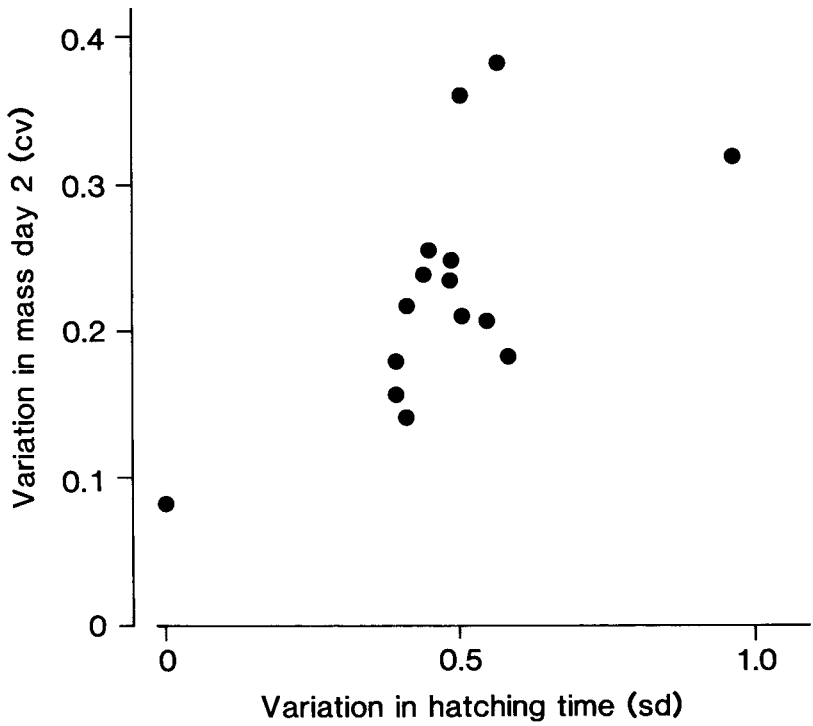

FIG. 1. The relationship between the coefficients of variation for nestling mass at two days post-hatching and the standard deviation of hatching spread. $r_s = 0.62$, N = 15, $P < 0.02$.

knew the masses of all hatched eggs that were also not subject to partial mortality before two days of age. The coefficient of variation in mass of nestlings two days after hatching was not affected by the coefficient of variation in egg mass ($F_{1,45} = 0.18$, $P = 0.68$). In fact, only 0.4% of the variation was explained by egg mass variation. The results were the same also when different brood sizes were analysed separately ($P > 0.1$ in all cases).

When estimating the persistence of size hierarchies, we only included broods where at least three nestlings still could be identified (from day 11 some nestlings lost their bands). We estimated the persistence of size hierarchies among nestlings in two ways. First, for each brood we related the mass of nestlings at varying ages to their mass when two days old. This analysis demonstrated that the relative sizes of nestlings were kept

TABLE 1

THE RELATIONSHIP BETWEEN NESTLING MASS AT VARIOUS AGES TO THEIR MASS WHEN TWO DAYS OLD TESTED WITHIN BROODS USING PEARSON CORRELATION

Age (days)	+[a]	−[a]	*P*
3	41	0	<0.0005
4	41	0	<0.0005
5	37	1	<0.0005
6	38	0	<0.0005
7	39	0	<0.0005
9	33	0	<0.0005
11	28	2	<0.0005
14	11	3	0.11

[a] The number of broods with positive and negative relationships at various ages.
[b] Significance tested with sign test.

until at least 11 days after hatching (Table 1). The lack of significance at 14 days of age is probably due to the decline in sample size caused by nestlings losing their bands. Interestingly, there was a tendency for the slope of the relationship between nestling mass at 11 days of age and that when two days old to be higher when brood size was higher (isotonic regression on slopes for broods of size 4, 5, and 6, $E_3^2 = 0.13$, $P = 0.063$; see also Fig. 2), indicating that hierarchies may be maintained to a higher degree when broods are larger. Secondly, we related the amount of variation in mass at various ages to the amount of variation at two days of age. These analyses showed that the magnitude of the mass hierarchy

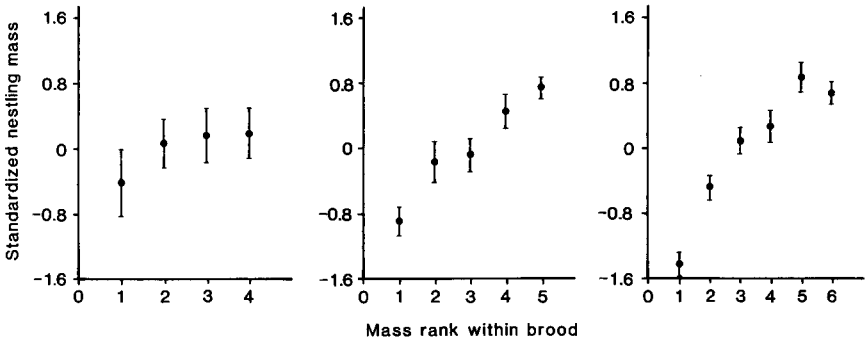

FIG. 2. The relationship between mass of nestling starlings when 11 days old and the relative rank of mass within broods (1 being the smallest) when two days old for broods of 4, 5, and 6 nestlings. Nestling mass was standardized to a mean of zero and a variance of one within broods.

TABLE 2

THE RELATIONSHIP BETWEEN THE COEFFICIENT OF VARIATION OF NESTLING MASS AT VARIOUS AGES TO THE COEFFICIENT OF VARIATION AT TWO DAYS OF AGE FOR STARLING BROODS

Age (days)	N	r^a	P
3	41	15.160	0.001
4	42	8.822	0.001
5	40	5.211	0.001
6	40	5.684	0.001
7	41	5.928	0.001
9	34	3.439	0.002
11	32	1.282	0.210
14	17	1.184	0.255

[a] Tested with linear regression.

within broods was affected by the magnitude two days after hatching at least up to day 9 (Table 2; Fig. 3).

DISCUSSION

Adaptive brood reduction in variable environments is thought to be facilitated by nestling size hierarchies (Lack 1947). These nestling size hierarchies are in turn thought to be affected by both hatching spread (Magrath 1990) and egg size variation (Slagsvold et al. 1984). Accordingly, egg size variation and variation in hatching spread have been interpreted as adaptive (e.g., Rydén 1978, Slagsvold et al. 1984, Hussell 1985, Slagsvold 1986).

According to the brood-reduction hypothesis, the last-laid egg should be smaller than the other eggs in the clutch (Slagsvold et al. 1984) to contribute to the development of nestling size hierarchies (Slagsvold et al. 1984). However, our study demonstrates that egg size variation has at the most a very weak effect on nestling size hierarchies. Other studies have also found that egg mass accounted for only a small proportion of the variation in nestling mass (Bryant 1978, Bancroft 1984, Stokeland and Amundsen 1988). Mead and Morton (1985) demonstrated for the White-crowned Sparrow (*Zonotrichia leucophrys*) that although the last-hatched chicks came from larger eggs, they turned out to be smaller than their siblings due to asynchronous hatching. It seems likely that variation in egg size within clutches of passerines is of minor importance for establishing weight hierarchies. Hence, rather than being interpreted adaptively, variation in egg mass within clutches might arise as a consequence of nutritional constraints on the female during egg-laying (Järvinen and Ylimaunu 1986, Slagsvold and Lifjeld 1989, Nilsson and Svensson 1993).

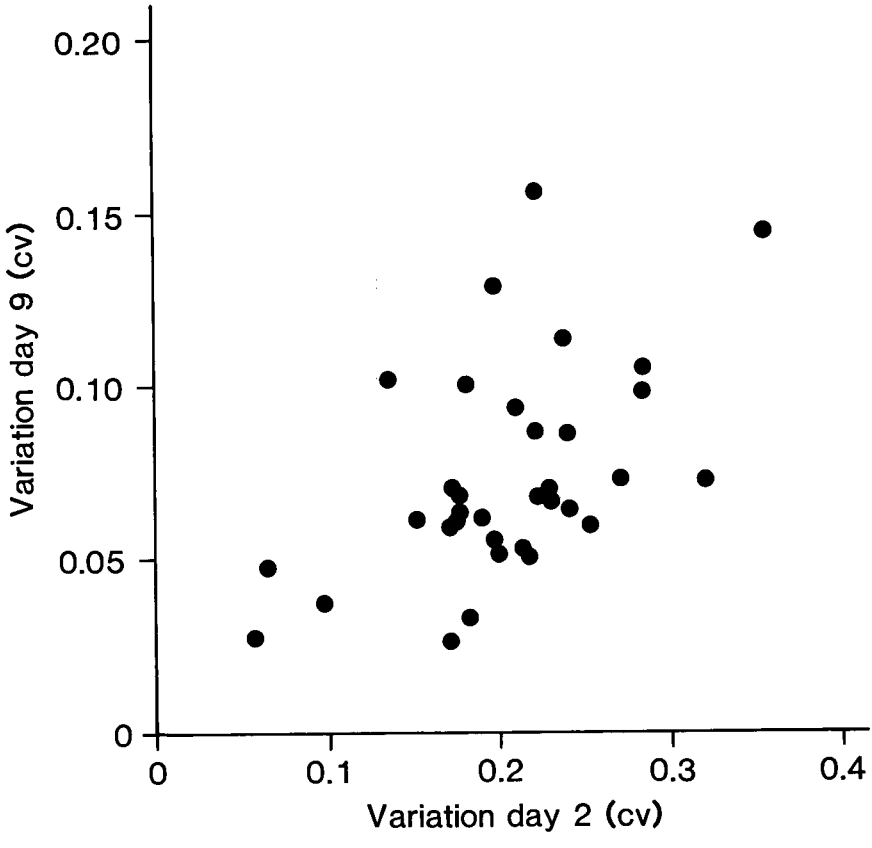

FIG. 3. The relationship between the coefficient of variation of mass within starling broods when nine days old to that of nestlings when two days old. For statistics see Table 2.

We found that the nestling size hierarchy among starlings reflected the hatching order of the chicks. Furthermore, the size of the hierarchy reflected the degree of hatching spread. Other studies also have shown that the most important reason for the development of weight hierarchies among nestlings is the difference in hatching time within the brood (Bryant 1978, Magrath 1992). This has also been experimentally confirmed for European Starlings by manipulating the incubation time of individual eggs (Stouffer and Power 1991). Hence, parents may determine the degree of mass variation within broods, and thereby the likelihood for brood reduction (Bryant 1978), by regulating at what stage they begin to incubate (Magrath 1992).

The initial nestling size hierarchy persisted during most of the nestling phase, but its importance decreased with the age of nestlings. Interestingly, the early size hierarchy tended to be more persistent in large broods. This could mean that sibling competition is more lax in smaller broods, enabling the smaller chicks to grow faster. Furthermore, in smaller broods nestlings might reach their asymptotic mass earlier.

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