Is hatching asynchrony beneficial for the brood?

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Many hypotheses have been proposed to explain why female birds start to incubate before clutch completion (IBCC). Some of those suggest that the resulting hatching asynchrony (HA) is adaptive because it increases the size hierarchy among offspring and in turn reduces nestling competition and energy demands during the peak feeding period. Others argue that IBCC is a good strategy in unpredictable environments. When food conditions deteriorate, the large size hierarchy quickly results in the death of the last hatched nestlings, allowing the remaining ones to survive and fledge in better condition. In comparison, under favorable conditions, all nestlings can fledge independent of hatching order. To test these hypotheses, we performed a brood size manipulation experiment (as a simulation of good and bad years) in collared flycatchers Ficedula albicollis and examined the effect of size hierarchy on offspring and brood performance. We found that chicks with an initial size disadvantage experienced reduced body mass growth and had shorter feathers at fledging in both reduced and enlarged broods. In enlarged broods, they also fledged with a smaller skeletal size. Although broods on average or parents could possibly still benefit from HA when food is scarce, this was not seen in the current study. Parental survival was not related to the size hierarchy in the broods, and the average body mass growth of the nestlings was slower in broods with a high initial size variance. We therefore conclude that HA and the resulting size hierarchy are probably detrimental for the growth of nestlings in both good and bad years, at least in species where nestling mortality does not occur early in life. Key words: collared flycatcher, fledging size, food supply, maternal effects, nesting growth, size hierarchy. [Behav Ecol 18:420–426 (2007)]

INTRODUCTION

Females in many bird species start to incubate their eggs before clutch completion (IBCC). This results in hatching asynchrony (HA) and in turn a pronounced size hierarchy among nestlings. Many hypotheses have been proposed to explain the adaptive function of this phenomenon (reviewed in Nilsson 1993; Stenning 1996). A large group of the explanations suggests that it is the established size hierarchy that increases the fitness of the parents and at least some of the offspring. The brood-reduction hypothesis (Lack 1954), for example, predicts that HA is advantageous in unpredictable environments. When food is abundant, all nestlings can fledge independent of hatching order. However, in cases of food shortage, older nestlings outcompete their younger siblings and, consequently, younger ones might quickly starve to death. By sacrificing the smallest nestlings, the rest of the brood can survive and fledge in better condition. This confers benefits both to the surviving young and the parents because fledglings in better condition might survive better (Pettifor et al. 2001) and therefore increase the fitness of their parents more than fledglings in poorer condition.

The sibling rivalry reduction hypothesis (Hahn 1981) predicts that in broods with an established size hierarchy among nestlings, sibling competition and thus energy expenditure of the nestlings are reduced. This results in faster growth or better body condition than in synchronous broods. Furthermore, the pronounced age hierarchy among siblings may reduce the peak energetic costs of the parents when feeding their young because nestlings reach their maximum growth rate and thus the highest food demand at different times (peak load reduction hypothesis: Hussell 1972).

Another group of the hypotheses argues that HA is only a by-product of IBCC, which is adaptive for reasons other than establishing sibling size asymmetry. If there is heavy nest predation or food resources are strongly declining during the chick-rearing period, IBCC can shorten the average time offspring spend in the nest (i.e., the combined length of the egg and nestling phase). Thus, females can reduce the risk of predation on their broods and prevent starvation at least of those nestlings which hatch and thus fledge earlier (hurry-up hypothesis: Hussell 1972; nest-failure hypothesis: Clark and Wilson 1981). According to the egg-viability hypothesis (Arnold et al. 1987; Veiga 1992), females start to incubate before completing their clutches in order to protect the hatchability of their eggs because the viability of unincubated eggs may decline with time.

When looking specifically at the effects of HA on the last hatched nestlings, it is often found that the size handicap with which these nestlings start their life results in disadvantages when competing for food (Ostreicher 1997; Pettifor et al. 2001). Thus, they might fledge with a smaller weight (Cotton et al. 1999; Clotfelter et al. 2000) or invest more testosterone of earlier onset of incubation, we might expect the parents to compensate for the detrimental effects of HA. Indeed, in several species with asynchronous hatching, females lay larger eggs at the end of the laying sequence (Howe 1976; Hillström 1999; Rutkowska and Gichoń 2005) or invest more testosterone in the last eggs to increase the rate of development (Schwabl 1996; Eising et al. 2001) and the competitive ability of the last hatched chicks (Schwabl 1993; Lípar and Ketterson 2000).

In our study species, the collared flycatcher Ficedula albicollis, previous studies have found successful compensation in terms of egg size for the detrimental effects of HA (Rosivall et al. 2005). However, egg volume increased with laying order only in years with a warm prelaying period, whereas in colder years, there was no such relationship (Hargitai et al. 2005). Because ambient temperature affects the availability of insect
and Råberg et al. (2005). Two explanations arise for the difference in the egg size pattern between good and bad years. First, females follow different strategies when they allocate nutrients into the eggs. This is because the adaptive value of size hierarchy differs between good and bad years with sibling size asymmetry being detrimental in good years but advantageous or neutral in bad years. Second, although compensation for HA would be beneficial independent of year type, because of energetic constraints during egg laying (i.e., less food is available) females are simply not able to lay larger eggs at the end of the laying sequence in poor years. To test the first hypothesis, we altered the rearing conditions of the chicks by conducting a brood size manipulation experiment and measuring the effects of size hierarchy on nestling growth, fledging size, and parental survival. Earlier studies have shown that though parents are to some extent able to adjust their provisioning rate according to the altered demand of their brood, which results in a change in workload, brood size manipulations can successfully alter the feeding rate to individual nestlings (for collared flycatchers see: Török and Tóth 1990; for other bird species see: e.g., Cronmiller and Thompson 1980; Nur 1984; Martins and Wright 1993) and change the level of nestling competition (Neuenschwander et al. 2003). Thus, enlarged and reduced broods have already been used to simulate years with good and bad years (Neuenschwander et al. 2003). Thus, enlarged and reduced broods with the same founding seasonal effects on nestling growth, the nests were selected so that the first egg was laid within an 8-day interval, and pairs of enlarged and reduced broods with the same hatching date were created. The original brood size of the brood pairs was the same in all but one case (in this case, the difference was one chick between the 2 broods). We partially cross-fostered broods 2 days after hatching so that 4 chicks were moved from nest A to nest B and 2 chicks were moved from nest B to nest A. As a result, we had enlarged (+2 chicks) and reduced (−2 chicks) broods consisting of approximately equal numbers of their own and foster chicks that were selected randomly with respect to their size. Each nestling was weighed on the day of swapping and marked individually by clipping tufts of down on its head and back. Body mass of the nestlings was measured from day 2 (day 0 = hatching date of the first chick) and the length of the third outer primary from day 8 (to the nearest 0.1 g and 0.5 mm, respectively) and on every second day until day 14. On day 14, tarsus length was also measured (to the nearest 0.1 mm).

### METHODS

#### Study species and field methods

The study was conducted in an artificial nest-box plot in the Pilis Mountains, Hungary (47°43'N, 19°01'E) in 2004. The study plot is part of a continuous, unmanaged, oak-dominated woodland, a protected area of Duna-Ipoly National Park. The collared flycatcher is a small hole-nesting, long-distance migratory passerine. Its breeding season starts in the middle of April, and females usually lay 5–7 eggs. The incubation period is about 12–13 days; nestlings hatch in a range from 12 to 44 h (mean ± standard error [SE] = 27.08 ± 1.32; Rosivall et al. 2005) and fledge 14–15 days after hatching.

Altogether, we studied 48 broods with the most common brood size being of 6 or 7 nestlings. Because the offspring of subadult and adult males might grow at a different rate (Hegyi et al. 2006), we only studied broods of adult males. One brood that was predated on day 4 was excluded from the analyses as were those broods that were secondary broods of polygynous males or reared by only one parent. The remaining 43 nests were retained for the analyses. To exclude the possible confounding seasonal effects on nestling growth, the nests were selected so that the first egg was laid within an 8-day interval, and pairs of enlarged and reduced broods with the same hatching date were created. The original brood size of the brood pairs was the same in all but one case (in this case, the difference was one chick between the 2 broods). We partially cross-fostered broods 2 days after hatching so that 4 chicks were moved from nest A to nest B and 2 chicks were moved from nest B to nest A. As a result, we had enlarged (+2 chicks) and reduced (−2 chicks) broods consisting of approximately equal numbers of their own and foster chicks that were selected randomly with respect to their size.

### Data analysis

We analyzed nestling growth and fledging size data both at the individual and brood levels in order to estimate the effect of HA and brood size manipulation on both the individual nestlings and the parental fitness.

In a data set collected in a previous study (for field methods, see Rosivall et al. 2005), it was found that the extent of HA in a brood was correlated with the coefficient of variation (CV) of the 2-day body mass when controlled for year (using general linear model (GLM): $F = 18.84$, degrees of freedom 1, $F = 8.84$, degrees of freedom 1, $F = 0.89$, respectively).

### Table 1

<table>
<thead>
<tr>
<th>Relationship of egg size and laying order</th>
<th>Predicted effect of HA on parental fitness/brood performance</th>
<th>Year-dependent female strategy</th>
<th>Energetic constraint</th>
</tr>
</thead>
<tbody>
<tr>
<td>Good year +</td>
<td>+/0</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Poor year 0</td>
<td>Not applicable</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>
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Displayed are F values with df in parentheses. Asterisks indicate the level of significance (**0.05, ***P < 0.005).

Table 2

The effects of relative size (CD), brood size manipulation (enlarged, reduced), and age on body mass of individual nestlings

<table>
<thead>
<tr>
<th>Effect</th>
<th>F (df)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>4922.78 (5,1482)**</td>
</tr>
<tr>
<td>Manipulation</td>
<td>5895 (1,1482)**</td>
</tr>
<tr>
<td>CD</td>
<td>680.20 (1,1482)**</td>
</tr>
<tr>
<td>Age × manipulation</td>
<td>833.82 (5,1482)**</td>
</tr>
<tr>
<td>Age × CD</td>
<td>22.18 (5,1482)**</td>
</tr>
<tr>
<td>Manipulation × CD</td>
<td>48.44 (1,1482)**</td>
</tr>
<tr>
<td>Age × manipulation × CD</td>
<td>6.49 (5,1482)**</td>
</tr>
</tbody>
</table>

Asterisks indicate the level of significance (**0.05, ***P < 0.005).

broods on day 2 (t1 = -0.69, P = 0.496). The average difference was 1.44 ± 0.13 and 1.30 ± 0.02 g (mean ± SE in enlarged and reduced broods, respectively), which corresponds to a hatching span of 30.65 and 29.22 h, respectively (the HA estimate is based on data from our earlier study on HA in this species [Rosivall et al. 2005]; equation of the linear regression HA = 16.04 + 10.16 × mass2dmax – min, where mass2dmax – min is the mass difference between the heaviest and the lightest chick at 2 days of age).

We also analyzed the effect of manipulation and the estimated HA on the survival of the parents. Because of the high site fidelity of breeding individuals (Könczey et al. 1992), we considered those individuals that were recaptured in 2 years after the experiment as survivors, whereas nonrecaptured birds as nonsurvivors. Survival was analyzed using generalized linear models with binomial error and logit link including manipulation category as a factor, size variation as a covariate, and the interaction of these terms. Because the dispersion parameter was larger than 1.0, we tested the significance of the parameters with an F-test (Crawley 1993); d-scale option was used in SAS 8.2.

RESULTS

Growth and fledging size of individual nestlings

To investigate the possible fitness consequences of nesting size hierarchy under different rearing conditions, we analyzed the effects of relative size of nestlings and brood size manipulation on body mass and feather growth rate and fledging sizes of the nestlings. The overall effects of these 2 variables and the interaction term were significant for all growth and fledging size parameters (Tables 2 and 3). Separate analyses of enlarged and reduced broods showed that initially smaller nestlings experienced slower body mass growth and smaller wing feather length at fledging in both manipulation categories (all P < 0.001; Figures 1a and 2b) with the disadvantage being larger in enlarged broods. However, feather growth rate, as well as the tarsus length and body mass of fledglings,

Table 3

The effects of relative size (CD) and brood size manipulation (enlarged, reduced) on feather growth rate and fledging size (body mass, length of the third outer primary, and tarsus length on day 14) of individual nestlings

<table>
<thead>
<tr>
<th>Effect</th>
<th>Feather growth</th>
<th>14d mass</th>
<th>14d feather</th>
<th>14d tarsus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manipulation</td>
<td>29.93 (1,192)**</td>
<td>17.30 (1,180)**</td>
<td>8.74 (1,180)**</td>
<td>11.00 (1,177)**</td>
</tr>
<tr>
<td>CD</td>
<td>4.39 (1,192)*</td>
<td>45.29 (1,180)**</td>
<td>305.90 (1,180)**</td>
<td>28.61 (1,177)**</td>
</tr>
<tr>
<td>Manipulation × CD</td>
<td>8.84 (1,192)**</td>
<td>52.08 (1,180)**</td>
<td>43.61 (1,180)**</td>
<td>24.54 (1,177)**</td>
</tr>
</tbody>
</table>

Displayed are F values with df in parentheses. Asterisks indicate the level of significance (**P < 0.05, ***P < 0.005).
Figure 1
a) Body mass growth of individual collared flycatcher nestlings in relation to their relative size \( \text{CD} = (\bar{a} - \bar{\bar{a}})/\bar{\bar{a}} \), where \( \bar{\bar{a}} \) = mean body mass of the brood on day 2, \( \bar{a} \) = the 2-day body mass of the chick in question. b) Average body mass growth in relation to initial size variation (CV) in collared flycatcher broods. Gray dots, dashed line: enlarged broods; black dots, solid line: reduced broods.
was affected only in enlarged broods (enlarged broods: all \( P < 0.006 \), reduced broods: all \( P > 0.548 \); Figure 2a,c).

**Average performance of the broods and survival of the parents**

With respect to parental fitness, brood performance may have a more important role than that of the individual nestlings. Therefore, we performed similar analyses as above to evaluate the effects of estimated HA on average nestling growth and fledgling size. We also analyzed how brood size manipulation and the magnitude of HA affected the survival of the parents.

Brood enlargement had an overall negative effect on body mass and feather growth rate and also on all measures of fledgling size (all \( P < 0.019 \)). However, estimated hatching span of the brood affected only the average mass growth so that a higher initial size variation resulted in slower body mass growth (Figure 1b, Table 4). Neither initial size variation of the brood (for females \( P = 0.908 \), for males \( P = 0.110 \)) nor brood size manipulation (for females \( P = 0.259 \), for males \( P = 0.105 \)) affected survival of the parents.

**Average growth and fledging size of the initially heaviest chicks**

According to some of the hypotheses proposed to explain the function of HA, it is also possible that the size hierarchy in the broods is beneficial only for nestlings with a competitive advantage. Therefore, we aimed to examine the effect of HA on nestlings with a higher rank in the size hierarchy.

We found that body mass and wing feathers of the 2 largest chicks grew slower in enlarged broods than in reduced broods (for feather growth rate: \( F = 19.55, \text{df} = 1,41, P < 0.001 \); for body mass growth: see Table 4), whereas brood size manipulation had no effect on the fledging sizes of these nestlings (all \( P > 0.402 \)). The estimated HA did not affect any of the growth and fledging size parameters (all \( P > 0.246 \)).

**DISCUSSION**

HA and the consequently established size hierarchy in the broods may have a pronounced effect on nestling growth (Cotton et al. 1999; Clotfelter et al. 2000) and survival (Forbes et al. 1997; Krebs 1999; Vinueza 2000). Therefore, it is not surprising that many hypotheses have been proposed to explain why females start the IBCC that leads to HA in the broods. These hypotheses can be divided into 2 groups

<table>
<thead>
<tr>
<th>Effect</th>
<th>Mass growth of the broods</th>
<th>Mass growth of the largest nestlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>646.38 (5,200)**</td>
<td>3613.71 (5,205)**</td>
</tr>
<tr>
<td>Manipulation</td>
<td>54.94 (1,40)**</td>
<td>26.81 (1,41)**</td>
</tr>
<tr>
<td>CV</td>
<td>6.18 (1,40)**</td>
<td>Removed</td>
</tr>
<tr>
<td>Age × manipulation</td>
<td>30.43 (5,200)**</td>
<td>20.91 (5,205)**</td>
</tr>
<tr>
<td>Age × CV</td>
<td>3.76 (5,200)**</td>
<td>Removed</td>
</tr>
<tr>
<td>Manipulation × CV</td>
<td>Removed</td>
<td>Removed</td>
</tr>
<tr>
<td>Age × manipulation × CV</td>
<td>Removed</td>
<td>Removed</td>
</tr>
</tbody>
</table>

Displayed are \( F \) values with df in parentheses. Asterisks indicate the level of significance (\( ^* P < 0.05, ^{**} P < 0.005 \)). Table shows the variables retained in the final model.
according to whether the established size hierarchy is considered to be adaptive or not (for reviews see Nilsson 1993; Stenning 1996). We investigated the adaptive value of size hierarchy in collared flycatchers F. albicollis by measuring nesting performance and parental survival. Earlier studies on this species have found maternal compensation for HA in terms of egg size in good quality years (Hargitai et al. 2005; Rosivall et al. 2005) but not in poor years. Therefore, we assumed that the size hierarchy may have different effects on parental and offspring fitness depending on environmental conditions, so that the size hierarchy is adaptive or neutral in bad years but detrimental in good years.

However, in our brood size manipulation experiment, nestlings with a relatively smaller size early in life suffered from reduced performance in both treatment groups. They gained body mass more slowly and had shorter wing feathers before fledging. The negative effects of small initial size were even more pronounced in enlarged broods where even feather growth rate and fledging size (body mass and tarsus length) were correlated with relative size on day 2. Despite these negative effects on individual nestlings, it is still possible that size hierarchy has beneficial effects at the brood level or for the parents. However, this study showed that average body mass growth of the brood was negatively affected by the initial size variation, and even nestlings with a competitive advantage did not benefit from HA.

We conclude that our results on nestling growth and fledging size in the 2 treatment categories do not support the predictions of the sibling rivalry reduction hypothesis (Hahn 1981). This hypothesis assumes that in broods with an established size hierarchy, siblings experience less severe competition and can therefore allocate saved energy into their maintenance. As a result, they should experience a better growth rate or fledge in better condition than those in synchronous broods. We have to note that unlike in our species, reduction in sibling rivalry may have important consequences on the growth and survival prospects of the offspring in species with direct aggression. Thus, we conclude that IBCC and HA are not beneficial for nestlings in the context of the resulting size hierarchy and suggest that females would benefit from compensating for HA irrespective of the quality of the current year.

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