

Senior and junior nestlings in asynchronous bluethroat broods differ in their effectiveness of begging

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ABSTRACT

In accordance with theoretical models of begging as an honest signal, empirical studies have found that begging by nestlings reflects need and that parent birds respond to variation in begging activity. However, parent birds hatch their broods asynchronously and the resulting within-brood size-asymmetries might induce differences in the begging tactics of senior and junior nestlings. In the present study, we tested for long-term effects of initial variation in size-asymmetry on food allocation, visual begging and physical competition among siblings by experimentally generating asynchronous and synchronous bluethroat (*Luscinia s. svecica*) broods. Seniors were fed more often than juniors. However, there were no differences in the pre-feeding begging behaviour of seniors and juniors. Thus, seniors were more effective at begging (i.e. had higher returns for a given level of begging) than juniors. There was no evidence that the higher effectiveness of seniors was due to juniors being excluded from the most favourable positions in the nest. Seniors in asynchronous broods might have been more effective at begging because they controlled food distribution through other behaviours than those analysed by us, or because parents preferentially fed seniors. Finally, we found that juniors begged for longer than seniors in asynchronous broods. This suggests that juniors compensated for their less effective begging by increasing their post-feeding begging effort. Our results provide evidence that marked initial size-asymmetries lead to a divergence in the begging behaviour of seniors and juniors.

Keywords: asynchronous hatching, food distribution, nestling begging, sibling competition, signalling of need.

INTRODUCTION

Offspring begging is suitable as a model system for studying animal communication when signallers and receivers have conflicting interests (reviewed in Kilner and Johnstone, 1997; Budden and Wright, 2001; Wright and Leonard, 2002). The interests of parents and their offspring are expected to diverge when parents and offspring are not genetically identical and care incurs costs to the parents (Trivers, 1974). Thus begging might have evolved as a strategy by which offspring attempt to extract more resources than parents are willing to provide (Trivers, 1974). Furthermore, when parents care for more than a single offspring at

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the same time, begging might have evolved as a means by which siblings compete for resources controlled by parents (Macnair and Parker, 1979). Godfray's (1991, 1995) signalling resolution models of parent-offspring conflict and sibling competition suggest that offspring begging can be honest if begging is costly and the benefits of being fed decrease with decreasing offspring need. The models predict that: (1) begging intensity reflects offspring need; (2) parents provide resources in relation to offspring begging intensity; and (3) offspring adjust their begging to the begging intensity of their siblings. Empirical studies have found good evidence for the first two predictions, whereas that for the latter is ambiguous (Kilner and Johnstone, 1997; Budden and Wright, 2001).

Parent birds often hatch their young asynchronously (Lack, 1947, 1954; Magrath, 1990; Stoleson and Beissinger, 1995). Lack (1947, 1954) argued that hatching asynchrony provides parents with a low-cost means of adjusting brood size in seasons with low food availability by establishing within-brood competitive asymmetries. Although alternative hypotheses for hatching asynchrony have been suggested (Magrath, 1990; Amundsen and Slagsvold, 1991a; Stoleson and Beissinger, 1995), it is well established that hatching asynchrony affects food distribution within broods, typically resulting in higher mortality of junior nestlings (e.g. Magrath, 1990; Stoleson and Beissinger, 1995; Amundsen and Slagsvold, 1998). Despite the considerable interest in asynchronous hatching and its consequences, surprisingly little is known about how parental and nestling behaviours interact to produce biases in nestling mortality (Amundsen, 1999). In particular, there is little information on variation in begging tactics employed by different-sized siblings. This is unfortunate because, as argued below, size-asymmetries might present begging models with some as yet unresolved problems (see also Godfray, 1995; Price *et al.*, 1996; Cotton *et al.*, 1999).

One potential effect of marked initial size-hierarchies is to induce within-brood variation in the effectiveness of begging (the return in parental resources for a given level of begging; Parker *et al.*, 1989). The benefit of begging to a nestling can be seen as the product of the benefit of receiving a food item (defined by the nestling's state) and the probability of receiving food when begging at a given level (i.e. the nestling's effectiveness of begging). Variation in the effectiveness of begging may arise when siblings compete physically for proximity to their parents, in which case juniors may be less effective at begging if seniors exclude them from the more favourable positions (Kilner, 1995; Cotton *et al.*, 1999). Furthermore, parents may gain information on nestling condition partly through nestling begging and partly through non-signalling cues, such as nestling size, which parents might assess directly (Redondo and Castro, 1992; Godfray, 1995). If this is the case, juniors might be less effective at begging because the parents, based on information gained through non-signalling cues, preferentially feed the seniors (Parker *et al.*, 1989; Godfray, 1995; Lotem, 1998a). Variation among nestlings in the effectiveness of begging might further affect nestling begging strategies if nestlings with a lower effectiveness of begging (e.g. juniors) compensate completely or partially for this disadvantage by increasing their begging effort.

Several studies have found that juniors receive less food than seniors even though the former beg more intensively (e.g. Kilner, 1995; Price and Ydenberg, 1995; Price *et al.*, 1996; Lotem, 1998b), suggesting that hatching asynchrony induces within-brood variation in the effectiveness of begging. From these observational studies, it is not clear whether the variation in begging behaviour is due to differences in nestling size *per se* or some confounding factor that affects both nestling growth and behaviour (e.g. egg size, hormonal titres or health/condition). Cotton *et al.* (1999) manipulated size-asymmetries in starlings (*Sturnus vulgaris*) to circumvent this problem. In asynchronous starling broods, seniors received

more food, begged for shorter durations and occupied positions closer to the nest entrance than juniors. This suggests that seniors had a higher effectiveness of begging than juniors because the latter were excluded from the most favourable positions. In synchronous broods, there were no differences between seniors and juniors. Cotton *et al.* (1999) experimentally fed the nestlings to control for potential differences in hunger between seniors and juniors. This design was used to separate the effects of relative size *per se* from other parameters of importance, such as hunger. The design is elegant, but the results cannot be applied directly to a natural setting in which seniors and juniors are likely to differ both in size and in hunger. To understand the dynamics of begging in the wild, experiments controlling for variation in hunger and studies examining begging behaviour when nestlings differ in both size and hunger are required.

The aim of this study was to assess the long-term effects of initial variation in within-brood size-asymmetry on the effectiveness of nestling begging in bluethroats (*Luscinia s. svecica*). We manipulated within-brood size-asymmetries in two directions early in the nestling period (day 3 after hatching): (1) *asynchronous broods*, in which seniors were 2 days older than juniors, and (2) *synchronous broods*, in which all nestlings hatched on the same day. We then tested for effects on food allocation, visual begging and physical competition later in the nestling period (day 8). A previous study based on the same experimental set-up found that the proportion of feedings was skewed in favour of seniors in asynchronous broods and more evenly distributed in synchronous broods (Smiseth *et al.*, 1998). However, it is unclear whether patterns of food distribution reflect differences in nestling behaviours. Seniors could have received more food in asynchronous broods simply because they begged more actively than juniors. Alternatively, seniors could have received more food without begging more actively either because they physically excluded juniors from positions near the parents or because the parents preferentially fed the seniors. Thus, we tested whether seniors in asynchronous broods begged more actively than juniors, or whether they monopolized frontal positions in the nest. If junior nestlings in asynchronous broods were less effective at begging, we expected them to compensate for this disadvantage by increasing their begging effort.

METHODS

Fieldwork was carried out during the nestling period in June–July 1995 in Øvre Heimdalen (61°25'N, 8°52'E; 1100 m above sea level), southern Norway. Male and female bluethroats feed their nestlings at similar rates (Anthonisen *et al.*, 1997; Smiseth *et al.*, 1998; Smiseth and Amundsen, 2000), except for the first days after hatching when females are engaged in brooding (Arheimer, 1982). Males and females do not differ in how they distribute feedings between senior and junior nestlings (Smiseth *et al.*, 1998). One or two nestlings are normally fed during each feeding visit. When two nestlings are fed, the second feeding appears to be very small compared with the first one (Smiseth *et al.*, 1998). The young fledge 10–13 days after hatching (Anthonisen *et al.*, 1997).

Brood manipulations

Within-brood size-asymmetry was manipulated by swapping nestlings between broods early in the nestling period (around day 3 after hatching) to generate two treatment groups (see also Smiseth *et al.*, 1998). Ten broods were made *asynchronous* so that they contained

two distinct size-classes of offspring, seniors and juniors, where seniors were approximately 2 days older than juniors (ratio of the seniors' body mass relative to that of the juniors on day 3 after hatching: 2.19 ± 0.14 , mean ± 1 standard error). Similarly, 10 broods were made *synchronous* so that they contained nestlings of similar size (ratio of the senior nestlings' body mass relative to that of the junior nestlings: 1.21 ± 0.03). The mean hatching span for the brood in the year of study was 1.1 days (range 0.5–2.0, $n = 14$; Hansen, 1997). Hence, the manipulations represented the extremes within the natural range of hatching asynchrony. Brood size was standardized to five nestlings, of which two or three were native to the nest. The mean brood size in the year of study was 5.3 nestlings (range 3–7; Hansen, 1997).

For the statistical analyses, nestlings of both asynchronous and synchronous broods were divided into two groups based on the nestlings' body masses immediately before the video recording. The two largest nestlings were always grouped as *senior* and the two smallest always as *junior*, whereas the intermediate nestling was assigned to the size category to which it was most similar with respect to body mass. Asynchronous broods were designed so that intermediate nestlings were always very similar either to the two seniors or the two juniors.

Asynchronous and synchronous broods were established simultaneously, thereby creating pairs of broods of the two treatments with the same mean age and brood mass. Thus, on what we refer to as day 8 after hatching (day 0 = day of hatching), asynchronous broods consisted of a mixture of nestlings 9 and 7 days of age, while synchronous broods consisted of nestlings 8 days of age. By filming the paired broods simultaneously, we controlled for potential confounds, such as weather, date and time of day.

Data recording

For each brood, we obtained a 3 h video recording of nestling begging behaviour on days 8 ($n = 18$) or 9 ($n = 2$) after hatching. We applied a dot of coloured non-toxic acrylic paint to the top of the head of each nestling to allow individual recognition during video analyses. Each nestling was assigned a unique colour that was chosen randomly in relation to its size-rank in the brood. We placed tripods at the nests 1 day before recording to habituate the parents to their presence. The video cameras were attached to the tripods in a position approximately 1 m from the nests and about 1.5 m above ground level. Bluethroats nest on the ground, typically under vegetation cover at the periphery of small bushes, and the entrance usually faces an opening in the vegetation (Arheimer, 1982). On the day before video recording, we removed vegetation obstructing the view of the nest from the camera position. The removal of some vegetation will inevitably cause minor changes in the microhabitat around the nest, potentially leading parents to feed from positions not used previously. Thus, to re-establish the restricted set of potential feeding positions that the parents were likely to use, we substituted the removed vegetation with small juniper branches placed in a semi-circle around the nest so as not to interfere with the video recording. This treatment ensured that the parents almost consistently fed the nestlings from the opening (personal observation). Under natural conditions, as well as after clearance of vegetation, bluethroat parents typically land several metres away from the nest and approach the nest on the ground from a highly predictable direction (personal observation). Thus, unlike some other birds (e.g. great tits *Parus major*; Kölliker *et al.*, 1998), bluethroat parents almost always enter the nest from the same position. Before video recording, we weighed all nestlings to the nearest 0.1 g using a Pesola spring balance.

Data analyses

From each video recording, we analysed nestling behaviour from the last 40 parental feeding visits. For each visit, we noted the time of parental arrival (defined as the moment the parent entered a zone that was less than one nest-cup diameter from the rim of the nest), the time of feeding and the time of parental departure. At the time of parental arrival, we noted *absolute nestling position* – that is, the position of the nestlings' beaks in relation to three sections of the nest cup. These sections were of equal width and perpendicular to the parental feeding position (1 = frontal, 2 = middle, 3 = distal). Because more than one nestling could occupy the same section of the nest cup, we also recorded *relative nestling position* – that is, the position of the nestlings' beaks ranked from 1 to 5 relative to the parents' feeding position (1 = closest, 5 = most distant).

We also recorded whether nestlings begged during the presence of a parent. If they did, we recorded the time they started to beg, the time they stopped to beg and the duration of interruptions in begging that occurred during the parent's presence. These data were used to produce four begging parameters:

1. *Begging frequency*: the proportion of feeding visits during which a nestling begged.
2. *Begging intensity*: the amount of body stretching performed by a begging nestling during the period from parental arrival to the time of feeding (1 = no stretching, 2 = stretching neck, 3 = stretching body, 4 = stretching body and tarsi). Several previous studies (e.g. Redondo and Castro, 1992; Lotem, 1998a,b; Cotton *et al.*, 1999) included absence of begging as the lowest value (typically scored as 0) in similar begging intensity indices, thereby not differentiating between begging frequency and variation in levels of begging when it occurs. This is not the case with our index.
3. *Begging start*: the time a nestling started to beg in relation to the time of parental arrival.
4. *Begging duration*: the summed duration of time a nestling begged during parental attendance (from arrival to departure from the nest, but excluding begging interruptions). Begging duration was only recorded for nestlings that were not fed during a visit. This was because a fed nestling occasionally stopped begging for the remaining period of that parental visit. The exclusion of these visits ensured that potential differences in the feeding success of seniors and juniors did not confound analyses on begging duration. Begging before parental feeding typically lasts less than 1 s, whereas begging may continue for 10 s or more after feeding (Fig. 1). Therefore, begging duration is likely to be a good estimator of begging effort.

All time measures were taken to the nearest 1/25 s (identical to one video frame). For all parameters, we calculated mean values for each nestling (over the 40 parental visits). We then calculated mean values for senior and junior nestlings to be used in the statistical analyses.

To test for effects of size-asymmetry and sibling size, we used a repeated-measures analysis of variance (ANOVA) with size-asymmetry (asynchronous *vs* synchronous broods) as a between-subjects factor and sibling size (senior *vs* junior) as a within-subjects factor. Data on begging frequency were arcsine square root transformed. All statistical tests were performed using StatView 5.0 and SuperANOVA 1.1. All *P*-values reported are two-tailed.

RESULTS

Nestling size and feeding rate per nestling

As intended, the brood manipulation on day 3 after hatching had a strong and lasting effect on within-brood size-differences (Fig. 1a). The difference in body mass between seniors and juniors was significantly larger in asynchronous than in synchronous broods (mean difference in body mass for asynchronous and synchronous broods: 4.7 ± 0.8 and 1.2 ± 0.2 g, respectively; paired t -test: $t_9 = 5.34$, $P = 0.0005$). The brood manipulation also affected the amount of food received by each nestling (Fig. 1b). A repeated-measures ANOVA revealed no significant effect of size-asymmetry on per capita feeding rates (Table 1), indicating that asynchronous and synchronous broods were fed at similar rates. Seniors were fed significantly more often than juniors, although there was no significant interaction between size-asymmetry and nestling size (Table 1). The lack of a significant interaction could be due to variation in confounding factors, such as weather conditions, as a paired comparison between asynchronous and synchronous broods recorded simultaneously found a significantly larger difference in feeding rate between seniors and juniors in asynchronous than in synchronous broods (paired t -test: $t_9 = 1.18$, $P = 0.048$).

Begging behaviour and physical competition

There was no evidence that size-asymmetries affected any of the begging parameters recorded, whereas nestling size-rank affected one parameter but not the others. We found no significant effects of the degree of size-asymmetry (asynchrony vs synchrony) on begging frequency, begging intensity, begging start or begging duration (Table 1, Fig. 2). Nor was there any significant difference between seniors and juniors in begging frequency, begging intensity or begging start (Table 1, Fig. 2). However, there was a statistically significant difference in the begging duration of seniors and juniors (Table 1), with juniors begging for longer than seniors (Fig. 2d). If within-brood size-asymmetries affected the begging dynamics among siblings, we would have expected an interaction effect of asynchrony and size-rank on begging. However, there was no significant effect of the interaction between size-asymmetry and nestling size on begging frequency, begging intensity or begging start

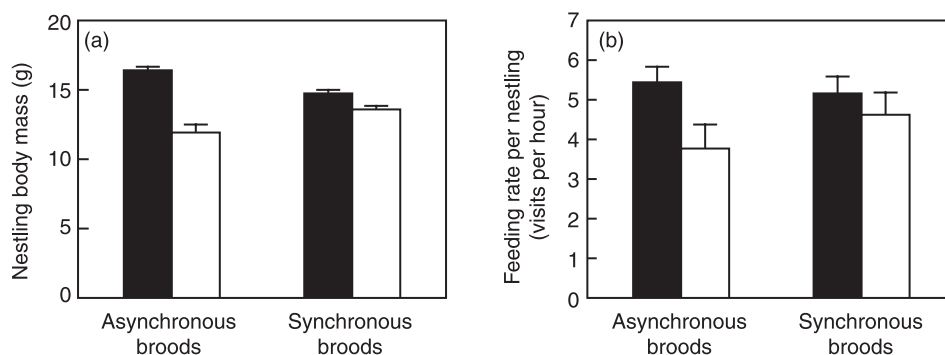


Fig. 1. (a) Nestling body mass and (b) feeding rate for senior (■) and junior (□) brood-mates in bluethroat broods of five nestlings manipulated to become asynchronous ($n = 10$) or synchronous ($n = 10$). Bars indicate mean ± 1 standard error.

Table 1. Tests for effects of size-asymmetry (asynchronous *vs* synchronous) and nestling size (senior *vs* junior) on *per capita* feeding rates, nestling begging and position occupied in the nest among bluethroat nestlings in broods of five

Variable	Size-asymmetry (asynchrony <i>vs</i> synchrony)		Nestling size-rank (senior <i>vs</i> junior)		Interaction (size-asymmetry $\times$ nestling size)	
	$F_{1,18}$	P	$F_{1,18}$	P	$F_{1,18}$	P
Parental feeding rates	0.22	0.65	8.45	0.009	2.50	0.13
Begging frequency	0.84	0.37	3.96	0.062	0.47	0.50
Begging intensity	0.88	0.36	0.003	0.96	0.68	0.42
Begging start	2.53	0.13	0.052	0.82	1.66	0.21
Begging duration	0.001	0.97	7.55	0.013	5.90	0.026
Absolute nestling position	0.054	0.82	0.31	0.59	0.68	0.42

Note: Repeated-measures ANOVA with size-asymmetry as a between-subjects factor and nestling size-rank as a within-subjects factor.

(Table 1, Fig. 2). These results suggest that hatching asynchrony had little or no effect on the begging behaviour of seniors and juniors before the time of feeding. However, we found a statistically significant interaction effect on begging duration (Table 1, Fig. 2d), indicating that hatching asynchrony affected the post-feeding begging effort of seniors and juniors differently.

Size-asymmetry had no detectable effect on competition for frontal nest positions, as demonstrated by the absence of any significant effect of the degree of size-asymmetry on absolute nestling position (Table 1, Fig. 2e). Furthermore, there was no significant difference in the absolute nestling position occupied by seniors and juniors (Table 1, Fig. 2e). Nor did nestling size-rank have a significant effect on the relative position occupied in the nest (Fig. 2f); seniors were not positioned any closer to the parents' feeding position than expected by chance (one-sample *t*-test; expected average relative position in a brood of five siblings = 3: $t_9 = 0.057$, $P = 0.96$ and $t_9 = 1.34$, $P = 0.21$, for asynchronous and synchronous broods, respectively). There was no significant interaction effect on absolute nestling position (Table 1, Fig. 2e), implying that seniors did not position themselves closer to the parents' feeding position in asynchronous than in synchronous broods.

DISCUSSION

We found that, with marked size-asymmetries among nest-mates, the distribution of food within the brood was skewed in favour of seniors. However, this was not related to any significant difference in visual begging between seniors and juniors before food was delivered, indicating that seniors were more effective at begging than juniors. Furthermore, there was no difference between seniors and juniors in the position occupied in the nest. Thus, there was no evidence that the higher effectiveness of begging by seniors in asynchronous broods was due to juniors being excluded from the most favourable positions in the nest. It is noteworthy, however, that seniors and juniors in asynchronous broods differed with respect to total duration of begging. The difference was due to an increased

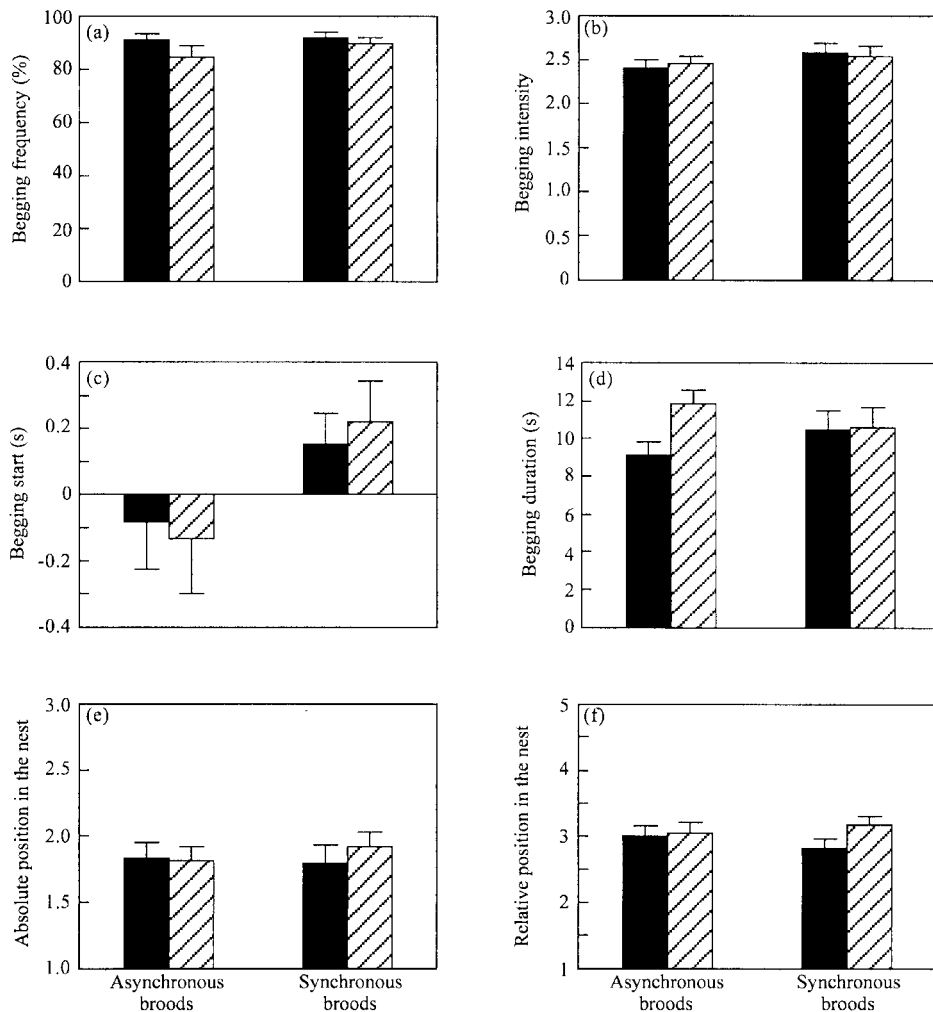


Fig. 2. (a) Nestling begging behaviour and position occupied in the nest of senior (■) and junior (▨) brood-mates in bluethroat broods of five nestlings manipulated to become asynchronous ($n = 10$) or synchronous ($n = 10$). The following behavioural parameters are shown: (a) begging frequency, (b) begging intensity, (c) begging start, (d) begging duration, (e) absolute nestling position and (f) relative nestling position. Bars indicate mean ± 1 standard error.

post-feeding begging effort of juniors, suggesting that juniors compensated for their less effective begging by increasing their begging effort. Below, we discuss the implications of our findings for the understanding of nestling begging strategies.

How do size-hierarchies affect food allocation?

We found a significantly larger difference in feeding rate between seniors and juniors in asynchronous than in synchronous broods. This is consistent with findings from a previous

study in which we found that seniors received considerably more food than juniors in asynchronous broods, whereas food was much more evenly distributed in synchronous broods (Smiseth *et al.*, 1998). Several previous studies on passerine species that hatch their young asynchronously have reported similar effects on food distribution (e.g. Price and Ydenberg, 1995; Lotem, 1998b; Cotton *et al.*, 1999). Thus, while large initial size-hierarchies had a marked effect on food distribution, subtle initial size-hierarchies had no detectable effect. This conclusion contrasts with the suggestion that even small initial size differences may be sufficient to generate significant divergence in size and consequent competitive superiority of seniors (Amundsen and Slagsvold, 1991b). In our study, juniors in the asynchronous broods were about 2 days younger than seniors. Parental provisioning tends to increase by nestling age in bluethroats, as in several other passerine birds (e.g. Alatalo *et al.*, 1982; Reinsborg, 1995; Wright, 1997). Therefore, the bias in food distribution could potentially reflect that seniors had higher short-term needs for food than juniors. However, this suggestion is contradicted by the finding that juniors spent significantly more time begging than seniors. This suggests that juniors had higher needs for food than seniors, possibly as a result of the skewed distribution of food in favour of seniors in asynchronous broods.

Why do senior nestlings receive more food?

We found no evidence for a difference in pre-feeding visual begging behaviour between seniors and juniors that could explain the skewed distribution of food in favour of seniors in asynchronous broods. The visual components of begging measured in our study are similar to those that have been found to reflect variation in hunger in other passerine species (reviewed in Budden and Wright, 2001). Furthermore, in bluethroats, individual nestlings beg significantly more often and for longer when hungry than when satiated (Eikenæs, 1999), suggesting that these begging parameters have the potential to carry information on nestling hunger. Seniors and juniors could have differed in terms of vocal, rather than visual, components of begging, as recently demonstrated in tree swallows, *Tachycineta bicolor* (Leonard and Horn, 2001). We did not record vocal components of begging because it is impossible to distinguish each nestling's vocalizations from our recordings. Hence, this possibility remains untested. In summary, our results demonstrate that, at least for visual begging signals, senior bluethroat nestlings in asynchronous broods were more effective at begging – that is, they obtained more food at a given level of begging – than juniors. Several previous studies have found that small nestlings receive less food than large ones even though the former beg more intensively (e.g. Kilner, 1995; Price and Ydenberg, 1995; Price *et al.*, 1996; Lotem, 1998b; Cotton *et al.*, 1999), suggesting that within-brood variation in the effectiveness of begging is widespread among passerine birds.

One hypothetical explanation for the greater effectiveness of begging by seniors in asynchronous broods could be that they excluded juniors from frontal nest positions. However, we found no evidence for this, as there was no difference between seniors and juniors in the positions they occupied in the nest. This finding contrasts with that of Cotton *et al.* (1999) on starlings, the only previous experimental study to test for effects of size-asymmetry on nestling begging strategies. In starlings, as in bluethroats, juniors in asynchronous broods begged for longer but received less food than seniors. In starlings, however, seniors occupied positions closer to the nest entrance, suggesting that they excluded juniors from positions near the parents. Another possible explanation for why

senior bluethroat nestlings obtained more food could be that they may have reached over the juniors. Begging height influences food distribution in some passerine birds (e.g. Leonard and Horn, 1996). Begging height is a composite trait that is determined by the amount of body stretching (i.e. begging intensity), which is a signalling trait, and body size. We found no evidence for an interaction between degree of size-asymmetry and nestling size on begging intensity. Thus, there was no evidence for a difference in the signalling component between seniors and juniors in asynchronous broods. However, seniors could have reached over juniors in asynchronous broods simply because they were bigger.

Finally, the higher effectiveness of begging of seniors might be caused by a parental preference for feeding seniors (Mock and Forbes, 1995; Forbes *et al.*, 1997). In deciding which nestling to feed, parents may integrate information on signalling (i.e. nestling begging) and non-signalling components (i.e. nestling size) (Redondo and Castro, 1992; Godfray, 1995). Parents might estimate nestling body size either directly (Redondo and Castro, 1992) or indirectly through gape size or colour (Kilner, 1997; Saino *et al.*, 2000). The marginal benefits to a parent would be higher from feeding a senior than a junior nestling if seniors have higher expected lifetime reproductive success. The principal strategy by which parents achieve a bias in food distribution in favour of seniors is the establishment of competitive asymmetries through asynchronous hatching (Lack, 1947, 1954; Mock and Parker, 1997). However, an emerging bias in food distribution in favour of seniors would inevitably lead to juniors becoming hungrier than seniors. Thus, if seniors cannot suppress the begging of juniors through physical exclusion from favourable positions or aggression, juniors might respond by increasing their begging activity. This, in turn, implies that if parents allocate food by use of begging signals only, the net effect would be a fairly even distribution of food within the brood. We therefore suggest that, in species where nestlings compete for food by using begging signals only, and not through physical competition or aggression (cf. Mock and Parker, 1997), parents might be expected to display more active feeding preferences for seniors. This may be the reason behind the skewed food distribution and the reduced success of juniors in asynchronous broods found in a variety of species (e.g. Magrath, 1990; Amundsen and Slagsvold, 1991a; Stoleson and Beissinger, 1995).

Why do junior nestlings beg for longer?

The only observed difference in the behaviour of seniors and juniors in asynchronous broods was that juniors begged for longer. Our aim was to test for long-term effects of initial size differences on nestling begging, and therefore we did not experimentally control for variation in nestling hunger. Consequently, we could not distinguish between the effects of nestling size and hunger state on begging duration. Because begging activity tends to increase with nestling age (Price *et al.*, 1996; Lotem, 1998a), the most likely explanation for why juniors begged for longer is that they were hungrier than seniors. However, it is not obvious why juniors should beg for longer as a consequence of being hungrier than seniors. This is because the parents deliver their food shortly after their arrival to the nest (0.62 ± 0.03 s; mean $\pm$ standard error) and seniors and juniors did not differ in when they started to beg. Thus, the increased begging duration was due to juniors begging for longer after the delivery of food. The average time spent begging after feeding in asynchronous broods was about 11 s for juniors and 8 s for seniors (Fig. 2d). Although parents frequently feed more than one nestling during a visit, most of the food is given to the first nestling fed

(Smiseth *et al.*, 1998). Hence, it is unlikely that juniors would benefit much from increasing their begging duration through food received at the current feeding visit.

An alternative explanation is that juniors begged for longer in an attempt to compensate for their less effective begging. Lotem (1998b) suggested that juniors should increase their begging effort when the parents show a feeding preference for seniors. The begging behaviour of nestlings that differ in the effectiveness of begging may diverge through learning, as a consequence of the difference in expected gains. A recent study supports this suggestion (Kedar *et al.*, 2000). We have no conclusive evidence to show why junior bluethroat nestlings responded by increasing their begging duration rather than their begging activity before feeding. One possible explanation is that juniors have little to gain from increasing their pre-feeding begging effort because of their lower ability to compete for the currently presented food item. If this is the case, juniors might be forced to increase post-feeding begging effort to induce the parents to increase their feeding rates. Parental feeding rates are likely to be affected by the summed begging stimuli from the brood. An increase in feeding rates could benefit juniors more than seniors because higher feeding rates would act to reduce the competition within the brood, which, in turn, could give juniors access to a larger share of the food. There is some evidence for this suggestion in blue-throats, as juniors received a smaller share when food was experimentally restricted (P.T. Smiseth, R.J. Bu, T. Amundsen and A.K. Eikenæs, submitted). Our results suggest that the increased post-feeding begging effort of juniors could compensate only partially for their less effective begging, because juniors still received less food than seniors.

CONCLUSION

Despite the considerable theoretical interest in the evolution of begging in the recent decade, several important theoretical issues are still not completely understood (Godfray and Johnstone, 2000; Wright and Leonard, 2002). One important issue concerns the effects of variation in nestling body size induced by hatching asynchrony on the signalling behaviour of seniors and juniors (see Cotton *et al.*, 1999). Our results suggest that marked size-asymmetries lead to a divergence in post-feeding levels of begging by seniors and juniors, but not in pre-feeding levels of begging. The similar pre-feeding levels of begging for seniors and juniors might reflect equal cryptic need (i.e. hunger) for both groups, or higher cryptic need for juniors, as suggested by the higher levels of post-feeding begging, accompanied by higher costs of begging for juniors.

Asynchronous hatching is widespread among birds (Magrath, 1990; Stoleson and Beissinger 1995). Thus, knowledge on the interaction between nestling behaviours (both begging and physical competition) and parental favouritism in asynchronous broods is essential to improve our understanding of the dynamics of avian reproduction. Research aimed at understanding the effects of within-brood size-asymmetries on offspring communication of need to their parents is in its infancy, and increased efforts in this field should be encouraged.

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