



# Hatching asynchrony and early nestling mortality: the feeding constraint hypothesis

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Several benefits may be gained from staggered hatching in birds but asynchrony sometimes appears to cause unnecessary starvation of the youngest nestlings. We present a solution to this paradox by suggesting that foraging parents are sometimes constrained by complex interactions between prey size, energy demands and foraging efficiency (the feeding constraint hypothesis). The requirement to provide smaller nestlings with small and soft food items while at the same time satisfying the greater food demands of larger nestlings may cause a conflict that results in the starvation of junior siblings. We examined the hypothesis in a field experiment where pied flycatchers, *Ficedula hypoleuca*, were video filmed while provisioning synchronous and asynchronous broods. Prey size and load size increased with nestling age suggesting that larger prey were more profitable to bring to the nest than smaller prey. Although small nestlings had difficulty swallowing large prey, parents of asynchronous broods brought large items suitable for the size of the older nestlings. Hence, junior nestlings suffered from reduced growth and increased mortality.

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In most species of birds where parents feed nestlings, the eggs in a clutch hatch not simultaneously but over a period of one or more days (Clark & Wilson 1981; Stoleson & Beissinger 1995). Younger nestlings in these asynchronous broods typically starve and die before older siblings. The most common view is that such mortality represents an adaptive reduction of brood size in response to food shortage or in case more than an optimal number of eggs hatched (Lack 1947; Magrath 1990; Mock & Parker 1997), letting marginal offspring track uncertain resources (Forbes et al. 2002). In many species with facultative brood reduction, parents seem to adopt 'laissez-faire' provisioning, allowing senior nestlings that are physically aggressive to monopolize food deliveries (Mock & Parker

1997). Even among passerines, there is abundant evidence that older nestlings may monopolize deliveries by securing positions in the nest closest to the provisioning parent (Leonard & Horn 1996).

Although brood reduction may sometimes be adaptive, a paradox is that in species without strong physical aggression such as many passerines, hatchlings often die in the first few days although food is sufficient at the time, and also appears sufficient for the parents to have reared the entire brood in the longer term (Price 1985; Slagsvold 1986; Amundsen & Stokland 1988). When nestlings are so young and immobile that they can only tilt their head upwards to gape, scramble competition to reach the provisioning parent can hardly explain the disadvantage of the younger brood members; parents supposedly control allocation. Thus, junior offspring suffer because parents either choose not to feed them or are somehow constrained from doing so. Despite the plethora of studies on begging in passerine birds, few have focused on food allocation to offspring 0–3 days old, despite this being the time when much of the mortality occurs.

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If hatching asynchrony is maladaptive as some hypotheses suggest (Magrath 1990; Stoleson & Beissinger 1995), parents may try to mitigate hierarchies by allocating more resources or hormones to later-laid eggs (Slagsvold et al. 1984; Schwabl et al. 1997) or by preferentially feeding the youngest nestlings in a brood (Stamps et al. 1985). We suggest that there may be occasions when parents wish to rear the entire brood, but are prevented from feeding small offspring because of constraints resulting from complex interactions between prey size, energy demands and foraging efficiency (the feeding constraint hypothesis). These constraints may lead to nonadaptive mortality of small nestlings. We focus on the mechanism that parents may face when providing smaller nestlings with small and soft food items while at the same time satisfying the increasing food demands of larger nestlings. We examined parental food allocation in a field experiment where the pied flycatcher, *Ficedula hypoleuca*, a small insectivorous passerine, was video filmed when provisioning synchronous and asynchronous broods.

### The Feeding Constraint Hypothesis

Many nestlings hatch at a developmental stage when they can ingest and digest only small and soft food items. Indeed, parents typically provide smaller food items to younger than to older nestlings (Royama 1966; Newton 1967; Kirkham & Morris 1979; Courtney & Blokpoel 1980). Smaller prey may contain special nutrients important for younger nestlings (Royama 1966; Newton 1967) or, more likely, be required simply because younger nestlings cannot swallow large prey, as seen in some terns, gulls and herons (Kirkham & Morris 1979; Courtney & Blokpoel 1980; Moser 1986).

We assume that parents foraging from a central place, all else being equal, prefer to capture and bring to the nest prey that are most profitable, usually larger prey. As nestlings grow and brood demands increase, there will be more pressure for parents to maximize energetic efficiency by satisfying the demands of larger nestlings with larger prey items. However, if only large nestlings, but not small ones, are able to use large prey items and a parent's foraging time is limited, this may come at a cost to the small nestlings and result in their deaths.

When filming the pied flycatcher, we looked for several provisioning patterns that would be consistent with the feeding constraint hypothesis. (1) If large prey are more profitable to bring to the nest than small prey, prey size will increase with nestling age and food demands, provided that the availability of different-sized items does not change. We did not measure prey profitability directly, but examined trends in the size of prey delivered to broods during the first 10 days posthatching. (2) However, we suggest that large food items may not be so abundant that parents can afford to satisfy the senior nestlings while simultaneously spending extra effort to provide small prey to junior nestlings. In this case, the variation in the size of prey brought to asynchronous broods should not be greater than the variation in prey size brought to synchronous broods (with 'senior' nestlings in both brood

types the same age). As a result, junior nestlings in asynchronous broods should suffer from poor growth and increased mortality compared to nestlings of the same age in synchronous broods. (3) Small nestlings have difficulty swallowing large prey. For prey items of a certain size, parents will take longer to transfer them to smaller nestlings than to larger nestlings. For nestlings of a certain size, parents will have more difficulty transferring large items and hard and bulky prey such as adult insects with wings and legs than soft flexible prey such as larvae. (4) The failure to provide food to small nestlings in asynchronous broods is not a deliberate parental strategy. If parents are choosing to ignore small nestlings, they should not attempt to feed them even when they are gaping. If feeding constraints are operating, we predict that parents may try, but fail, to deliver large prey to small nestlings, and that this prey will be directed subsequently to larger brood members. This may provide a proximate explanation for why younger nestlings starve although the total demand for food by the brood has apparently not reached its peak. In older asynchronous broods, when gape sizes are nearly adult size, parents will have no problems transferring prey to junior nestlings.

### METHODS

The pied flycatcher is a secondary cavity nester that feeds the young mainly with insects and spiders. Males and females are of similar size. The modal clutch of six eggs usually hatches over 1 day but asynchrony may span up to 5 days (Creutz 1955; Slagsvold 1986; Slagsvold & Lifjeld 1989; Amundsen & Slagsvold 1991) so parents are adapted to variable degrees of asynchrony. We studied flycatchers breeding in nestboxes in deciduous woodland near Oslo, Norway (60°00'N, 10°38'E). Food provisioning to synchronous and asynchronous broods was filmed through an opening on one side of the nestbox in June 2003 and 2004. Nestling age was judged from daily inspection of nests at hatching and from body mass (Slagsvold 1986).

### Synchronous Broods

Synchronous broods consisted of eight unmanipulated broods from 2003 and 16 experimentally synchronized broods from 2004 which we created by transferring eggs or newly hatched young between nests. Nestlings were transferred in 2004 to control for handling effects relative to the asynchronous broods (see below). In both years, early nestling mortality, before the young were 4 days old, occurred in only two of eight broods in 2003 and in two of 16 broods in 2004. Pied flycatchers are tolerant of human disturbance at the nest and we have no reason to think that our visits and manipulations influenced prey choice and feeding behaviour. Hence, the synchronous broods from 2003 and 2004 were pooled in all analyses but we controlled for year effects in some tests. For the synchronous broods ( $N = 24$ ) the mean date of the first egg laid + SD was 8 May + 8, the mean clutch size + SD was 6.3 + 0.6 eggs, the mean brood size on day 1 + SD was 5.3 + 1.1 young, and the mean hatching spread (after

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