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Hatching asynchrony in Linnets: the effects of nest predation and food demand of nestlings

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In this paper, we investigate hatching patterns and nestling growth in the Linnet *Carduelis cannabina*. We evaluate five possible hypotheses to explain the evolution of facultative hatching asynchrony in this species. Both synchronous and asynchronous hatching was observed in the Linnet, with small broods hatching synchronously and large broods hatching mainly asynchronously. Nest predation seemed to cause higher mortality in the late nestling stage compared to the mortality before incubation, which may explain the observed synchronous hatching of small broods. Asynchronous hatching resulted in increased weight hierarchies within broods, but was not associated with brood reduction, as implied by the traditional brood reduction hypothesis. Asynchronously hatched young had higher growth rates than synchronous young, indicating the importance of reducing competition between siblings or reducing peak load in food demands by asynchronous hatching when brood sizes were large. This study thus suggests a mixture of two strategies: synchronous hatching to reduce the risk of nest predation when the brood size is small (nest failure hypothesis), and asynchronous hatching to enhance growth conditions of young when the brood size is large (peak load and/or sibling rivalry hypothesis).

1. Introduction

In many altricial bird species eggs hatch asynchronously over a period of one or more days, depending on the time in the egg laying sequence that incubation starts (Clark & Wilson 1981). Hatching asynchrony implies that females start incubating before the clutch is completed, whereas incubation of synchronous broods only starts after the last egg has been laid. Many hypotheses have been proposed to explain the adaptive significance of asynchronous hatching, with Lack's (1947, 1954) brood reduction hypothesis being the most widely invoked explanation. However, the adaptive significance of asynchronous hatching is still subject to much speculation and research. Stoleson and Beissinger (1995) reviewed 17 distinct hypotheses that have been advanced to explain hatching asynchrony in birds. Here we investigate the pattern of hatching asynchrony in Linnets *Carduelis cannabina*, a bird species showing facultative hatching asynchrony. The breeding ecology of Linnets fits the scenarios and requirements of only a subset of the 17 hypotheses reviewed by Stoleson and Beissinger (1995). For instance the Energy constraint hypothesis (Slagsvold 1986, Moreno 1989) is not relevant in species where the male supplies all food resources

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to the female during incubation (Stoleson & Beissinger 1995), as is the case in Linnets (Newton 1972). Likewise, the brood parasitism hypothesis (Wiley & Wiley 1980, Kendra et al. 1988) is not relevant for Linnets, since neither inter- nor intra-specific brood parasitism occur (J. Drachmann unpubl.). The following five hypotheses could potentially explain hatching asynchrony in Linnets.

(1) The Brood reduction hypothesis: Lack (1947, 1954) proposed that when food levels during the breeding season are unpredictable, birds should lay the clutch size they are able to raise under good breeding conditions but hatch the clutch asynchronously. The resulting age hierarchy within the brood would then imply that the youngest chick would have a competitive disadvantage due to its smaller size. When food resources are low, this chick will quickly starve and the brood will be reduced to an optimal size.
(2) The Peak load reduction hypothesis: This hypothesis proposes that asynchronous hatching is a means of reducing the workload of parents by spreading the peak food demand of individual nestlings over time (Hussell 1972, Bryant 1978).
(3) The Sibling rivalry hypothesis: By asynchronous hatching parents can impose a stable dominance hierarchy among brood members. They thus avoid wasteful scramble competition between siblings (Hahn 1981), and make more efficient use of parental resources regardless of food availability.
(4) The Sexual conflict hypothesis: Beginning incubation before the end of egg-laying may be a tactic that permits females to increase the parental effort of their mates. Early incubation increases the time that females sit on eggs, and asynchronous hatching lengthens the time that females brood young nestlings. Thus, the total time during which males must provision food to their mate is greater in asynchronous broods than in synchronous broods (Slagsvold & Lifjeld 1989).
(5) The Nest failure hypothesis: This hypothesis suggests that asynchronous hatching reduce the probability of total brood loss by predation. By incubating before completing the clutch, parent birds may speed up the time of fledging for at least some young (Hussell 1972, Clark & Wilson 1981).

The aim of this paper is to describe the pattern of hatching asynchrony and nestling growth in Linnets and to evaluate the relative importance of the different hypotheses proposed to explain asynchronous hatching.

2. Methods

2.1. Study species and study areas

The Linnet (family Fringillidae) is a socially monogamous and multi-brooded passerine with biparental care. Linnets are non-territorial granivorous birds that often forage socially on communal feeding areas, and the nestlings are predominantly raised on seeds (Newton 1972, personal observations). The nest is built solely by the female, and dense coniferous trees are preferred as nest sites. All incubation is done by the female, who is dependent on her mate's ability to feed her during incubation (Newton 1972).

Data for this study were collected from late April to early August in 1993–1996 at two sites in Denmark. In 1993–1995 we studied a Linnet population at Sjellemosegaard (SMG, 56°10′N, 9°50′E), a 12.7 ha Christmas tree plantation with young Caucasian Firs *Abies nordmanniana*. In 1995–1996 another population was studied at Langholm (LH, 56°30′N, 10°50′E), approximately 70 km from SMG. This study area consisted of five ha dominated by Cypress *Chamaecyparis lawsoniana* and Common Spruce *Picea abies*. The Linnets arrived at the study areas in April, with the first clutches being laid in late April or early May. The breeding season continued until late August, resulting in two or three broods per breeding season. Until mid May the Linnets fed on seeds from last year, but as soon as seeds of *Taraxacum* ripened they switched to a diet of new seeds, and hatching of the first broods always coincided with *Taraxacum* seed ripening (J. Drachmann unpubl.). Later in the season, the parents fed on seeds from a variety of families such as *Compositae*, *Cruciferae* and *Geraniaceae*, which they found both within and several kilometres outside the study areas. In both study areas, several nests were lost due to nest predation by Hooded Crows *Corvus corone cornix* and Magpies *Pica pica*.

2.2. General field procedures

Nests were located by observing parental birds with nesting material, by simply searching the vegetation, or by detecting copulating pairs, since copulation usually takes place near the nest (Drachmann et al. 1997). Nests were followed until fledging of nestlings or until the nest had been lost due to desertion or predation. During egg laying and at the time of hatching most nests were visited daily. Artificial nest experiments conducted at SMG in 1995 showed that frequent nest visits by humans did not influence the risk of nest predation (J. Drachmann, M. M. Broberg & P. Søgaard in prep.). The daily nest visits made during egg laying and hatching in this study did therefore probably not influence the results presented here.

After hatching, the nestlings were marked with a permanent marker on different toes for individual identification. Approximately every second day, between 12.00 and 14.00, the mass of each nestling was measured to the nearest 0.5 g with a 50 g Pesola spring balance. When the nestlings were 10 days old, they were large enough to leave the nest if disturbed. Nestlings that disappeared after 10 days of age were therefore considered to have fledged, unless the nest showed signs of predation or other kinds of mortality. The weight of eight days old nestlings (WD8) was used as an indicator of fledging weight, since weights of most nestlings could be obtained at this age. After WD8 was measured, the nestlings obviously put on more mass before they fledged, especially the lightest nestlings. However, when comparing nests with different brood sizes and hatching patterns, it seemed reasonable to assume that WD8 gave a reliable index of the relative differences among nests in fledging mass. Fledging mass is a relevant fitness component since fledging mass and postfledging survival have been shown to be positively correlated in many bird species (reviewed in Magrath 1991). Disappearance and death of single nestlings and their position in the size hierarchy were recorded when observed.

In order to evaluate the Peak load reduction hypothesis it was important to have information on the workload of the parents when provisioning the young. To get an estimate of the variation in food demand of nestlings, the provisioning rate of parents during the first eight days after hatching was filmed on video. Due to a high nest predation rate (J. Drachmann, M. M. Broberg & P. Søgaard in prep.), we only succeeded in filming parental feeding behaviour at one nest, which contained six asynchronously hatched young. Compared to insectivorous birds, the granivorous Linnet parents provisioned their young at a relative low rate (see results). In order to obtain precise estimates of parental feeding rates, daily provisioning rates were therefore calculated as the number of observed daily feeding visits divided by the total number of observation hours.

2.3. Data analyses

A generalised linear model (GLM) with a poisson error distribution and a log link function was used to investigate the influence of study area, year and season on clutch size. Linnets tended to lay larger clutches during mid-season, and therefore a quadratic function of day of first egg was used as a predictor variable in the analysis of seasonal effects on clutch size.

Because there was no difference between the two areas and among years in clutch size and nestling growth parameters, the pooled data from both areas and all years were used in the analyses. However, the frequency of nest-predation differed between the two areas, but not between years (J. Drachmann, M. M. Broberg & P. Søgaard in prep.), and the data on nest predation was therefore analysed for the two areas separately.

Information on hatching intervals was important in the evaluation of all five hypotheses. Therefore, regular daily nest visits during hatching in 1996 were used to estimate hatching intervals. If all eggs hatched between two consecutive visits (within 24 hr), hatching was considered synchronous. If all eggs hatched between 24–48 hr or 48–72 hr, the hatching was considered asynchronous, and the hatching intervals considered being two or three days, respectively. However, even frequent visits made to a nest give only an approximate value of hatching intervals (Bryant 1978, Richter 1984). The relative difference in nestling mass (RDNM) was therefore used to describe the size hierarchy at hatching, i.e. the weight hierarchy and not the difference in age was used as a measure of hatching asynchrony. The difference in nestling mass (DNM) was calculated as the mass of the heaviest minus the mass of the lightest chick, and RDNM was then calculated as DNM divided by the mean mass of all brood members. The mean mass of brood members and DNM were, depending on hatching spread, measured two or three days after hatching of the first egg, and all nestlings were measured on the same day. Broods with a RDNM > 0.45 were considered to be asynchronous, and broods with a size hierarchy less than that value were considered to have hatched synchronously. This threshold value was in agreement with the observed hatching intervals (see results), and the value given by Skagen (1987) for American Goldfinches *Carduelis tristis*, a closely related cardueline finch. With RDNM being normally distributed, the effects of brood size and season (day of first egg) on this variable were analysed with a GLM assuming a normal error distribution and an identity link function.

In the evaluation of the Brood reduction, Peak load reduction and Sibling rivalry hypotheses it was important to compare growth rates and fledging weights of differently sized nestlings in asynchronous and synchronous broods. Nestlings were therefore divided into groups according to mode of hatching (synchronous or asynchronous) and position in the size hierarchy at hatching (lightest, intermediate and heaviest young). This was done based on the RDNM at hatching, measured when nestlings were 2 days old. Individual growth rates and fledging weight (WD8) were estimated for the lightest, the intermediate and the heaviest nestling in each brood. Growth rates were based on changes in weights from 2 to 11 days of age, since nestling growth was approximately linear in this interval. The slope of fitted regression lines was used as an estimator of individual growth rate by which nestlings of different positions in the size hierarchy at hatching could be compared. The effects of brood size, hatching pattern, nestling size hierarchy, and season (day of first egg) on nestling growth rate and WD8 were evaluated by GLM-analyses with a normal error and an identity link function, since both of these dependent variables were normally distributed.

Under the Nest failure hypothesis it is not the absolute rate of nest failure that is important, but rather the nest failure ratio, i.e. the ratio of the daily probability of nest failure during the nestling period relative to the daily probability of failure during the egg period (Clark & Wilson 1981). The relevant parameters for testing this hypothesis are the probability of nest loss during laying and fledging, because the time from onset of incubation to the first hatch and from the first hatch to the first fledge does not depend on when incubation is initiated (Hussell 1985). In our study, most nests were found prior to the onset of incubation, but some nests were not. Daily survival probabilities were therefore estimated by Mayfield's (1975) method, and their standard errors were calculated by Johnson's (1979) formula. Nest survival probabilities were calculated for the period from the first egg to the start of incubation and for the period when the first young reached an age of 10 days until the last young reached that age.

Not all data obtained during the four years of study could be used in the analyses due to various restrictions. Some of the broods were measured too late (nestlings more than 2 days old) to estimate their RDNM at hatching. In addition, when estimating individual growth rates, only nestlings that were measured at least three times were included in the analysis. Finally, some broods were predated before WD8 could be determined and only nests in which all eggs hatched were used to analyse the relationship between hatching type and nestling growth. Consequently, sample sizes varied in the different analyses and information on the relevant sample sizes is given for each analysis. All statistical analyses were performed in accordance with Zar (1999) and Crawley (1993). Results are presented as means ± SE and differences were considered significant at $P < 0.05$.

3. Results

3.1. Clutch size

There was no significant difference in clutch size between the two study areas or among years (GLM-analysis: $\chi^2_2 = 0.151$, $P = 0.22$, and $\chi^2_1 = 0.113$, $P = 0.29$ for area and year, respectively), and the mean clutch size was 5.05 ± 0.06 (n = 133, range 3–7) for all years and areas pooled. Clutch sizes of three were only encountered three times and a clutch size of seven was only observed once during 1993–1996. There was a significant seasonal variation in clutch size (GLM-analysis: [Day of first egg]^2: $\chi^2_1 = 0.951$, $P = 0.002$), with a mid-season peak in the end of May and beginning of June (Fig. 1).

3.2 Hatching intervals and relative difference in nestling mass (RDNM)

Observed hatching intervals ranged from one to three days in both areas. Hatching intervals could be estimated with certainty in eight clutches, and therefore only these clutches were used to relate hatching type and RDNM values. Four of these clutches hatched asynchronously (RDNM > 0.45), whereas the other four clutches hatched with certainty within 24 hr (RDNM < 0.45). The precise RDNM-values for these eight nests are shown in Fig. 2 as a function of the actual hatching spread. The RDNM of 2-day-old nestlings could be estimated for 33 broods in 1993–1996, showing that 42% of these broods were asynchronous (Table 1). There was a significant effect of brood size on RDNM (GLM: $F_1 = 12.70$, $P = 0.001$), with broods being more variable in mass when brood size increased (Fig. 3). Timing of breeding did not influence the hatching pattern, since no seasonal effect was found on RDNM (GLM: $F_1 = 3.41$, $P = 0.08$). Fitting a quadratic function of day of first egg to the model did not show any significant seasonal trends either.

3.3. Provisioning rates

For the male there were two pronounced peaks in nestling provisioning rate, one directly after hatching and a second peak when the nestlings became older than seven days (Fig. 4). Fitting male feeding rate as a quadratic function of day after hatching showed that the two peaks in male provisioning rate were statistical significant (GLM: [Day]^2: $F_2 = 30.83$, $P = 0.001$). In the first days after hatching all food provisioned by the male was delivered to the brooding female that subsequently fed the small nestlings. In contrast to male provisioning, the female provisioning rate did not exhibit any pronounced variation (GLM: $F_1 = 7.659$, $P = 0.07$).

3.4. Growth rates in relation to size hierarchy

Growth rates of the lightest, the intermediate and the heaviest nestlings were estimated for 31 broods in 1993–1996 (Fig. 5). Brood size had a highly significant effect on nestling growth rate (Table 2), with growth rate declining almost 50% from 1.64 g/day in broods with four young to only 0.84 g/day in nests with seven young. The growth rate was also significantly different between synchronous and asynchronous broods ($P = 0.03$), with asynchronous broods having a higher growth rate than synchronous broods (Fig. 5). Likewise, there was a significant difference in individual growth rate between the different nestling size categories ($P = 0.003$), i.e. the growth rate increased with nestling size (Fig. 5). The significant interaction between brood size and position in the size hierarchy was because the difference in growth rate between the lightest young and the other nestlings increased considerably for brood sizes larger than five. There was no seasonal effect on growth rate (Table 2), but a significant interaction between season and brood size because of the effect of season on clutch size (Fig. 1). Fitting a quadratic function of day of first egg to the model gave a similar non-significant effect of season.

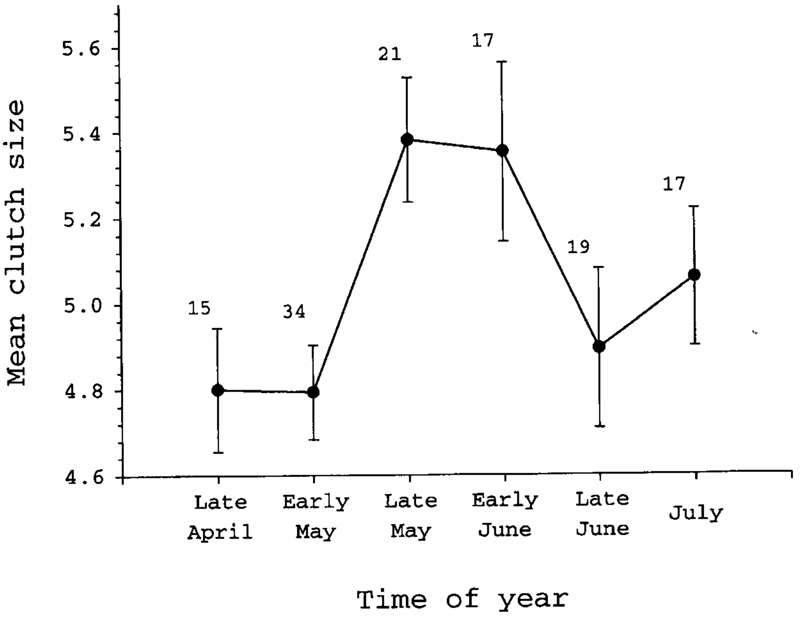

Fig. 1. Seasonal variation in mean (±SE) clutch size when the breeding season was divided into half-month intervals, except for July where the sample size was smaller. Values above error bars indicate sample size.

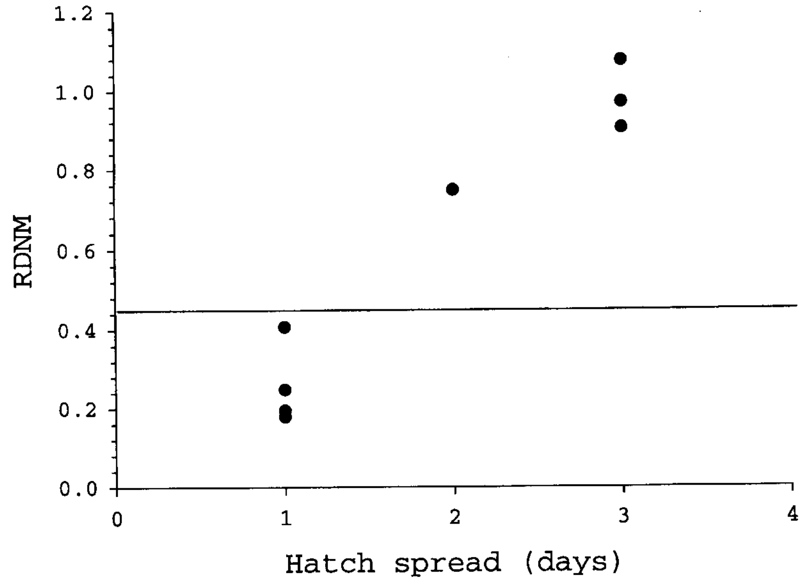

Fig. 2. The relative difference in nestling mass (RDNM) at two days of age as a function of hatching spread (n = 8).

3.5. Weight of eight days old nestlings (WD8) in relation to size hierarchy

WD8 of the lightest, the intermediate and the heaviest nestlings could be estimated for 21 broods in 1993–1996 (Fig. 6). Brood size had a highly significant effect on WD8 (Table 2), which declined from 13.54 g to 7.48 g when the brood size increased from four to seven young. A significant difference in WD8 between the different nestling size categories was also found (P = 0.0001, Fig. 6). Thus, the lightest nestling at hatching was still significantly lighter than the other brood members when eight days old, which was in accordance with the significantly smaller growth rate of the lightest nestlings (Fig. 5). The significant interaction between position in the size hierarchy and brood size (P = 0.0002) was caused by a relatively larger effect of brood size on WD8 of the lightest nestlings than on the intermediate and heaviest nestlings. No overall significant difference was found in WD8 between synchronous and asynchronous broods (Table 2). There was, however, a significant interaction between brood size and hatching type (P = 0.03), because synchronous broods had a higher WD8 than asynchronous ones for brood sizes of five and below, while asynchronous broods obtained the highest WD8 for brood sizes larger than five. There was no overall effect of season on WD8, but a significant interaction between brood size and season due to the non-linear relationship between these two variables shown in Fig. 1. As for growth rate, adding a quadratic function of day of first egg to the analysis did not improve the fit of the model.

3.6. Nestling mortality and nest predation

Twenty-seven nests with 136 nestlings could be followed until the nestlings fledged. Most other nesting attempts failed due to nest predation (78% of nests at SMG and 30% at LH, J. Drachmann, M. M. Broberg & P. Søgaard in prep.). Only two out of these 136 nestlings died during the nestling stage, one from a brood of four nestlings and the other from a brood of six nestlings. Both broods hatched synchronously, and brood reduction by the death of the smallest chick was thus rare, and not associated with asynchronous hatching.

The daily survival probabilities in the two periods relevant for the Nest failure hypothesis, the time from first egg to incubation and the time from first young aged 10 days to last young aged 10 days, are shown in Table 3 for SMG and LH. Survival was higher in the fledgling stage than prior to incubation in SMG, while the opposite was true for LH, where the egg stage prior to incubation had the highest survival. However, these differences were non-significant (using the test proposed in Johnson (1979): P > 0.15), because sample sizes were small and standard errors were strongly dependent on nest-days of exposure. Therefore, no clear conclusions could be drawn on the relative risk of predation in the early egg stage and the late nestling stage. The survival probability in the fledgling stage for LH were, however, based on a larger sample size than the value for SMG, and not biased by zero values, and therefore probably more reliable. This would indicate a slightly higher mortality around fledging than prior to incubation, although non-significant.

4. Discussion

Parents often feed those nestlings that gape the highest and quickest (e.g. Bengtsson & Ryden 1983), and the video recordings of parental provisioning showed that this was also the case in Linnets. The observed size hierarchies within Linnet broods were thus not only caused by asynchronous hatching, but also by differential feeding of the young, which explained why size hierarchies also occurred in synchronous broods near the time of fledging (Fig. 6). Here we evaluate the relative importance of the five possible hypotheses for the evolution of hatching asynchrony in Linnets.

The Brood reduction hypothesis (Lack 1947, 1954) predicts that, when food is scarce, late hatched nestlings in asynchronous broods should be more likely to die, than the smallest nestlings in synchronous broods, so that unproductive parental investment in surplus young is minimised. In this study there was no significant difference in growth rate of the lightest brood member of asynchronous and synchronous broods (Fig. 5), and death of the lightest brood member was only recorded in two synchronous broods. Brood reduction was thus rare in Linnets, and was not facilitated by asynchronous hatching, which makes the Brood reduction hypothesis invalid in Linnets.

Table 1. The distribution of synchronous and asynchronous hatching in relation to brood size. Based on RDNM, synchronous: RDNM < 0.45, asynchronous: RDNM > 0.45.

Brood size	Synchronous	Asynchronous
3	1	0
4	4	0
5	10	7
6	4	6
7	0	1

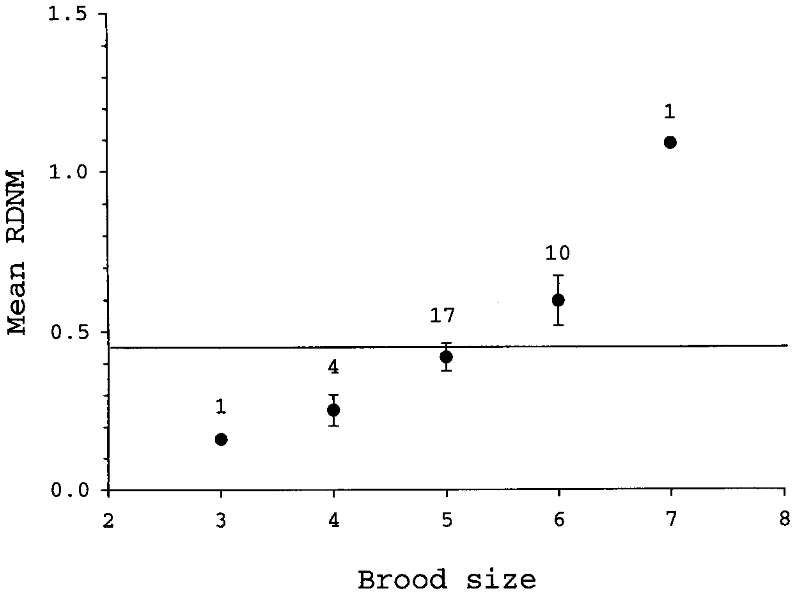

Fig. 3. Hatching interval as a function of brood size. Hatching interval was measured as mean (± SE) relative difference in nestling mass (RDNM) at hatching. Broods with RDNM < 0.45 were classified as synchronous and broods with RDNM > 0.45 as asynchronous. RDNM = 0.45 is indicated by the line in the figure. Numbers above error bars indicate sample size.

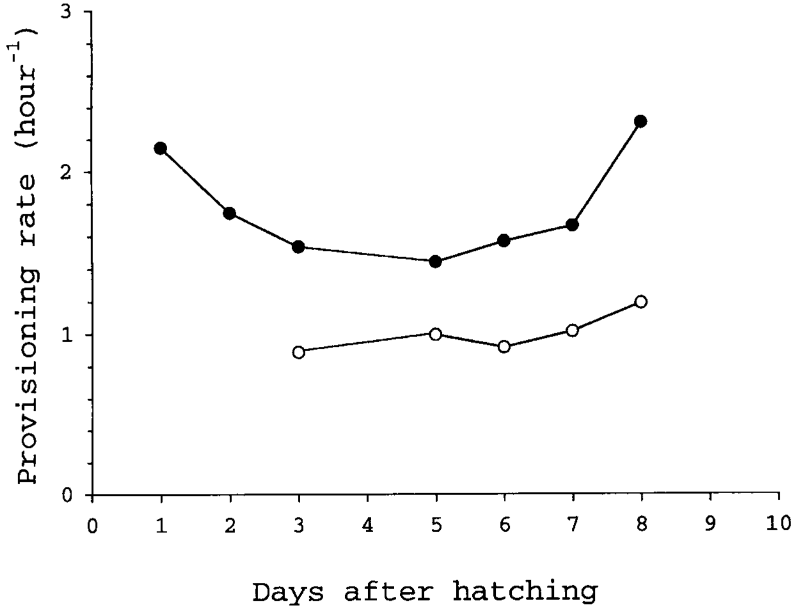

Fig. 4. Provisioning rates of male (black dots) and female (open dots) Linnets to an asynchronous brood of six young (Day 0 = Day of hatching). The daily provisioning rates were calculated as number of daily feeding visits divided by the total number of observation hours.

Under the Peak load reduction hypothesis, the decisive advantage of asynchronous hatching is the extension of the overall hatching time. The parents are then able to stagger the time of peak food demands of their individual offspring, and thereby reduce the maximum amount of food to be provided on a given day (Hussell 1972, Bryant 1978). This hypothesis requires that during growth each nestling has a period of peak food demand, after which its requirements decline. Our analysis of parental provisioning rates was only based on data from one nest. Fig. 4, however, suggests the possibility that food requirements of Linnet nestlings, measured as parental feeding rate, were highest for very young nestlings (1–2 days old), and then increased again in the late nestling stage.

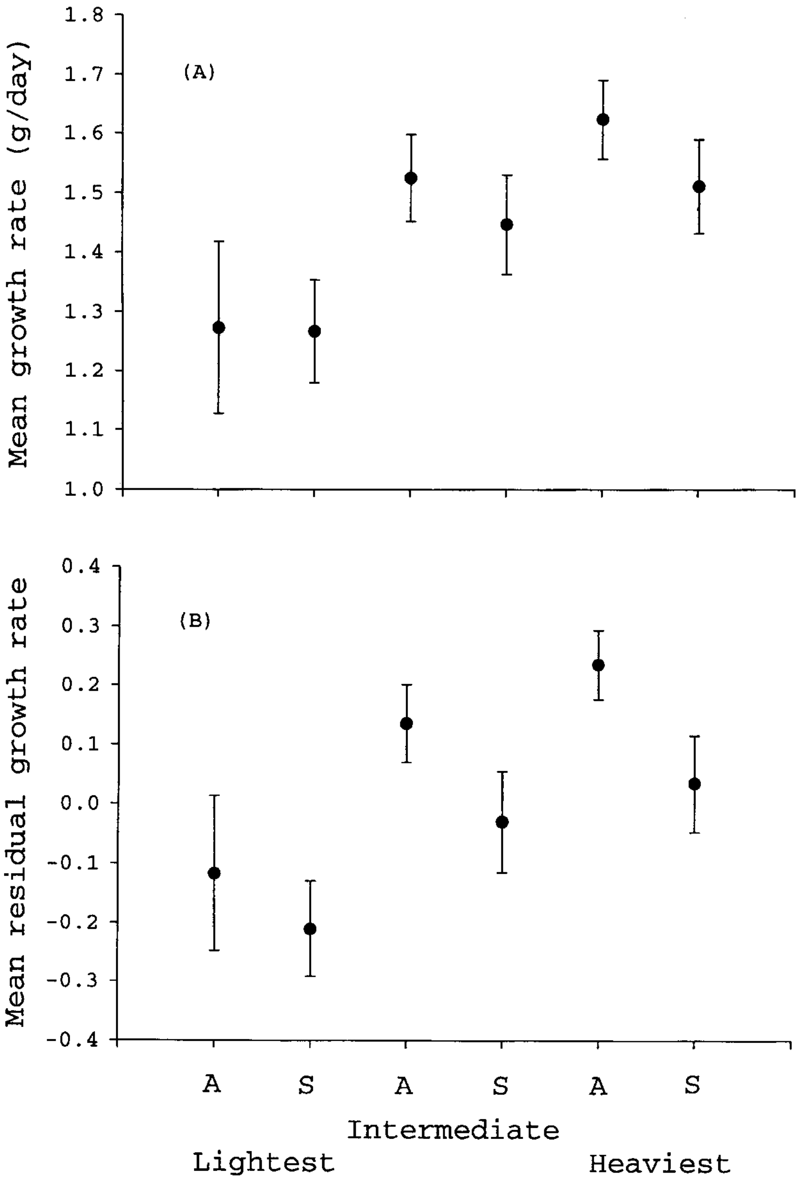

Fig. 5. A: Growth rates of nestlings in relation to their relative size at hatching (lightest, intermediate and heaviest) in 17 synchronous (S) and 14 asynchronous (A) broods. B: Same data as in A, but after controlling for the effect of brood size on nestling growth rate: the residual values from a linear regression of nestling growth rate on brood size are given. All values are means (± SE).

Unfortunately, no estimate of parental provisioning rates of synchronous broods was obtained, but according to the Peak load reduction hypothesis, Fig. 4 may have shown an even steeper pattern for synchronous broods. The small hatchlings require a high provisioning rate because digestive efficiency is low in small nestlings of seed-eating finches (Glück 1988). Older nestlings can digest their food more efficiently, and the increased provisioning rate in the late nestling stages was thus most likely due to increased energy demands for maintaining and increasing body weight before fledging. The parents could therefore possibly avoid an energetic bottleneck by hatching the brood asynchronously and spreading out the two periods of peak food demand across nestlings. It would especially be an advantage for the male, since he was the sole provisioner during the peak food demand of the small nestlings. Our findings support this hypothesis, since nestling growth rate was significantly higher in asynchronous than in synchronous broods (Fig. 5). The total peak food demand of the entire brood increases with brood size, and according to the Peak load reduction hypotheses an increase in asynchrony with brood size would be expected (Stoleson & Beissinger 1995). RDNM showed a sharp increase with brood size in the present study (Fig. 3). Both hatching pattern and nestling growth rate in Linnets thus support the Peak load reduction hypotheses. Mock and Schwagmeyer (1990), however, showed that the conditions favouring asynchronous hatching based on peak load reductions are very restrictive. Brood sizes have to be very large, hatching has to be very asynchronous and the steepness of the food requirement curves of individual nestlings needs to be very high. Mock and Schwagmeyer (1990) concluded that these conditions are rarely met in passerines. Our study did not confirm whether Linnets are an exception to this rule, but it seems likely that the low digestive efficiency of the small hatchlings may increase the steepness of the food requirement curve of individual nestlings. Thus, a reduction of peak load requirements may occur through asynchronous hatching of large broods in the Linnet.

According to the Sibling rivalry hypothesis, parents can avoid wasteful scramble competition between their offspring by hatching the eggs asynchronously (Hahn 1981). By asynchronous hatching parents can create a stable dominance (size) hierarchy among nestlings, and thereby make more efficient use of parental resources regardless of the food supply. Such avoidance of scramble competition between nest mates may be relevant for Linnet broods. One would expect the advantage of competition reduction, and thus hatching asynchrony to increase with brood size, which was the case in this study (Fig. 3). Both the Sibling rivalry hypothesis and the Peak load reduction hypothesis predict that asynchronous hatching is an adaptation to increase the growth conditions of the young by making parental behaviour more efficient (Stoleson & Beissinger 1995). We were, however, not able to distinguish between the two hypotheses in the present study.

Table 2. GLM-analyses of the effect of brood size (BS), hatching type (A/S = asynchronous/synchronous), position in the weight hierarchy (L/I/H = lightest, intermediate, heaviest) and season (Day = day of first egg) on nestling growth rate and nestling weight at eight days of age (WD8). Only significant interactions are shown.

	Growth rate			WD8		
Effect	F	df	P	F	df	P
BS	11.26	1	0.001	14.68	1	0.0003
A/S	4.784	1	0.031	1.831	1	0.1813
L/I/H	6.234	2	0.003	21.81	2	0.0001
Day	0.009	1	0.754	0.7879	1	0.3785
BS × Day	8.939	1	0.004	26.77	1	0.0001
BS × L/I/H	3.233	2	0.044	10.20	2	0.0002
BS × AS	-	-	-	5.031	1	0.0291

The female Linnet is dependent on her mate's ability to feed her during incubation (Newton 1972) and the male also delivers the food for the young directly to the female during the brooding period. Linnets thus fit the assumptions of the Sexual conflict hypothesis, which suggests that asynchronous hatching is a female strategy to increase the total time the male is going to provision her during incubation and brooding (Slagsvold & Lifjeld 1989). However, if asynchronous hatching was a result of a sexual conflict, we would not expect the hatching spread (RDNM) to be so strongly dependent on brood size, since any female, independent of brood size, would benefit from an increased provisioning by her mate. Additionally, asynchronous hatching may also be in the interest of the male, as it reduces his peak workload during the early nestling stage. This argument is unlikely to be violated by uncertainty of paternity, as extra-pair young are rare in Linnets (J. Bønløkke-Pedersen, J. Drachmann, J. Frydenberg, & J. J. Boomsma in prep.). Therefore, the Sexual conflict hypothesis seems also unlikely as a major explanation for hatching asynchrony in Linnets.

The Nest failure hypothesis applies to cases in which nest predation is heavy and continuous over the lifetime of the nest. Relative to synchronous hatching, asynchronous hatching reduces the amount of time that a nest contains only eggs, and reduces the amount of time before the first chick fledges, but increases the total amount of time a nest contains nestlings (Stoleson & Beissinger 1995). Asynchronous hatching is thus allowing for the possibility for partial nest predation, by letting the first hatched young fledge as early as

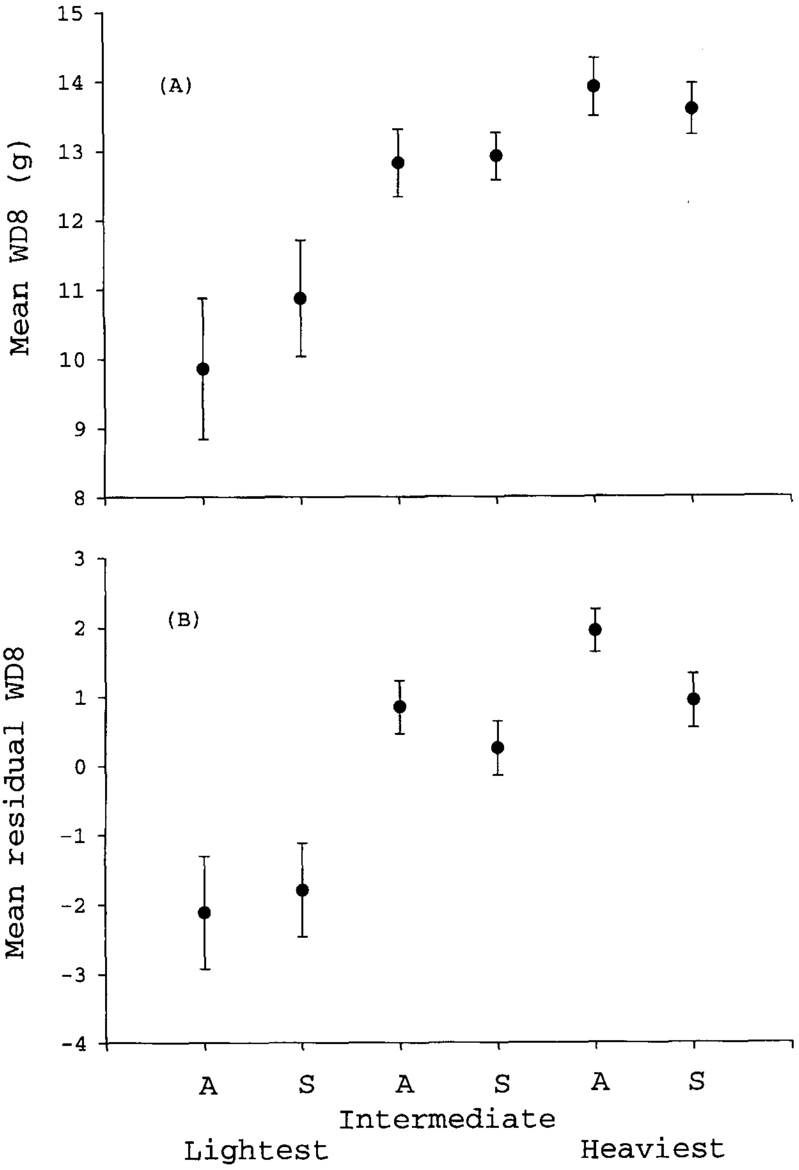

Fig. 6. A: Mean nestling weight at eight days of age (WD8) in 11 synchronous (S) and 10 asynchronous (A) broods. Nestlings were grouped, as in Figure 4, according to their position in the size hierarchy at hatching. B: Same data as in A after controlling for the effect of brood size on WD8: the residual values from a linear regression of WD8 on brood size are given. All values are means (± SE).

Table 3. Daily survival probabilities ± SE at Sjellemosegaard (SMG) and Langholm (LH) in the two periods: (A) from first egg to incubation and (B) from first young aged 10 days to last young aged 10 days. There was no significant difference between period A and B within study areas.

Area	Period	No. of nests	No. of nest-days	No. of losses	Daily survival
SMG	A	108	321.5	7	0.9782 ± 0.0081
SMG	B	20	22	0	1.0*
LH	A	54	161	1	0.9938 ± 0.0062
LH	B	31	32	2	0.9375 ± 0.0428

* SE could not be calculated, since no nests were lost in this period.

possible (Hussell 1972). Clark and Wilson (1981) argued that birds often suffer a higher degree of nesting failure during the nestling stage, and that synchronous hatching, which shortens the time during which nestlings are present in the nest, is therefore favoured. Asynchronous hatching is favoured when nest predation is higher in the egg-laying period (prior to incubation) than the fledgling period, or when predation is equal in the two periods. The fact that there was no significant difference in predation risk between the two periods in our study (Table 3), therefore suggests that the high observed predation level would favour asynchronous hatching. However, many of the broods did hatch synchronously (especially small brood sizes) which regardless of brood size would be incompatible with the high predation favouring asynchrony. The nest failure ratio was difficult to analyse properly in this study, since the high absolute nest predation gave low sample sizes of surviving nests in the late nestling stage (Table 3). However, if we take the tendency found for LH, as representative for the study populations, the higher (although non-significant) mortality in the late nestling stage compared to the mortality prior to incubation would favour synchronous hatching. This might explain why clutches of three to five eggs mostly hatched synchronously. In most cases, parents with brood sizes below six were probably able to raise the nestlings successfully without needing the extra advantage of asynchronous hatching (increased growth conditions of young). In clutch sizes of three to five synchronous hatching would thus be favoured if it reduced the nest predation in the late nestling stage. Contrary to this, when clutch sizes exceeded five asynchronous hatching was favoured in order to raise the young successfully, due to the advantage of either spreading out the peak food demands of nestlings or reducing the competition between nestlings. The clutch size variation in Linnets may thus reflect a trade-off between offspring number and predation risk. The lack of any seasonal variation in growth rate and WD8, but a significant mid-season peak in clutch size (Fig. 1), also suggested a trade-off between offspring number and offspring size during this period of the breeding season. The relatively smaller fledging weight associated with the increased brood size during mid-season may be compensated for by improved post-fledging conditions for young during mid-summer. It was, however, not possible to investigate this hypothesis further during the present study.

This study suggests that a mixture of two strategies might explain the hatching pattern in the Linnet: reducing the risk of nest predation in the late nestling stage when brood size favours synchronous hatching, and increasing growth conditions of young when brood size imposes asynchronous hatching. On average brood sizes larger than five seemed to favour asynchronous hatching. However, there was no fixed threshold brood size above which asynchronous hatching was always favoured (Table 1). The hatching strategy of individual pairs was probably also influenced by parental quality, and there was a considerable variation in parental provisioning ability among pairs (J. Drachmann unpubl.). Whether the increased growth conditions of asynchronous hatched young are ultimately due to a reduction in peak load requirements or to reduced sibling competition needs further experimental study.

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Selostus: **Hempon haudontatavat ja poikasten kasvu Tanskassa**

Kirjoittajat arvioivat viiden eri hypoteesin sopivuutta hempolla esiintyvän haudonnan asynkronian selittäjänä. Asynkroninen haudonta tarkoittaa sitä, että emo (hempolla naaras) alkaa hautomaan munia ennen kuin kaikki munat on munittu pesään. Sen sijaan synkronisissa pesissä haudonta alkaa vasta silloin kuin viimeinen muna on munittu pesään. Kirjoittajat seurasivat sekä synkronisia että asynkronisia hemppopesyeitä Tanskassa 1993-1996. Pienet pesyeet haudottiin synkronisesti ja suuret pesyeet pääasiassa asynkronisesti. Pesäpredaatio aiheutti suurempia pesätuhoja pesäpoikasvaiheen loppuaikana kuin ennen haudonnan alkamista. Tämä tekijä voi selittää pienten pesyeiden synkronisen haudonnan. Asynkroninen haudonta johti suurempiin poikasten välisiin painoeroihin pesyeissä, mutta asynkroninen haudonta ei johtanut pesyekoon pienenemiseen niin kuin perinteinen "brood reduction"- hypoteesi ennustaa. Asynkronisesti haudottujen pesien poikaset kasvoivat nopeammin kuin synkronisesti haudottujen pesyeiden poikaset. Tutkijoiden tulokset viittaavat siihen, että hempolla toimisi yhtäaikaisesti kaksi haudontastrategiaa : synkroninen haudonta, joka vähentää pesäpredaatiota pesyekoon ollessa pieni ("nest failure"-hypoteesi) ja asynkroninen haudonta, joka lisää poikasten kasvua pesyekoon ollessa suuri ("peak load" ja/tai "sibling rivalry"-hypoteesi).

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