Influence of hatching order on growth rate and resting metabolism of kestrel nestlings

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Hatching asynchrony in altricial birds may result in a competitive disadvantage for the youngest nestlings compared to older siblings. We studied the effects of a size hierarchy on the growth rate of Eurasian kestrels *Falco tinnunculus* chicks in nests with and without access to supplemented food in western Finland. Body mass stopped increasing on the 19th day after hatching while body size, estimated by a combination of bone and feather lengths continued to increase at least until fledging at 26 days. Body condition, reflecting muscle and fat, did not change markedly during the growth period from the 12th day to fledging. Body temperature and resting metabolism were usually lower in nestlings 12 days old than in nestlings at fledging. Growth of body mass, size and condition, and resting metabolism were delayed in last-hatched nestlings aged 19 days. Just before fledging, last-hatched nestlings attained a similar body mass and size, and had a similar resting metabolism to those of older siblings. At fledging, only in nests without access to supplemented food was the body condition of last-hatched chicks lower than that of its siblings, but in nests with access to supplemented food no such difference was detected. Our results highlight that the level of lipids in the last-hatched nestling can be affected by the food restriction imposed by hatching order.

Hatching asynchrony is a common feature in altricial birds that occurs when incubation begins before clutch completion (Clark and Wilson 1981, Magrath 1990). A hatching span of more than one day leads to a size hierarchy of nestlings within a brood, resulting in a competitive disadvantage for the youngest nestlings compared to older siblings, which in turn can lead to slower growth and higher mortality in the former (see O’Connor 1978, Ricklefs 1982, Zach 1982, Mock 1984). Lack (1954) suggested that hatching asynchrony may be adaptive because it could increase parental reproductive success when prey abundance fluctuates unpredictably (the brood reduction hypothesis). Whereas the brood reduction hypothesis did not predict whether the oldest young would show some signs of food shortage, the offspring quality assurance hypothesis states that asynchronous hatching is adaptive because it ensures adequate growth and high quality of at least some offspring (Slagsvold 1986, Amundsen and Stokland 1988, Amundsen and Slagsvold 1991). Numerous papers have studied offspring quality by determining the mean fledging mass in relation to food abundance (restricted or not; e.g. Bird and Lagüe 1982, Korpimäki 1988, Lacombe et al. 1994, Negro et al. 1994, Korpimäki and Rita 1996, Bukacinski et al. 1998, Durant and Handrich 1998) and to hatching order (Magrath 1989, Amundsen and Slagsvold 1991, Platteeuw et al. 1995, Wiebe 1995, Wiebe and Bortolotti 1995).

The reduction of effects of stochastic variation in food abundance on growth rate and fledging mass is one of the major reasons for a flexible pattern of growth. Postnatal growth usually shows an asymmetri-
The area consists of smaller agricultural fields surrounded by coniferous forests (Korpimäki and Norrdahl 1991, Korpimäki and Rita 1996, Korpimäki and Wiehn 1998). On open agricultural land, kestrels bred in nest-boxes mounted on barns and solitary trees. Kestrels in northern Europe are migratory and arrive at breeding sites from late March to early May (Village 1990, Palokangas et al. 1992). Their main prey items are voles (field vole Microtus agrestis, sibling vole Microtus rossiaemeridionalis syn. M. epiroticus and bank vole Clethrionomys glareolus) (Korpimäki 1985, 1986). The densities of these small mammals fluctuate in 3–4-year cycles with an amplitude of up to a 100-fold within a cycle (Korpimäki and Norrdahl 1991). Compared to biannual (May and September) snap-trapping data from 1973–99 (Norrdahl and Korpimäki 1995, Klemola et al. 2000), vole densities were very low in spring and summer 1998, which means food was scarce during the kestrel’s entire breeding season. In 1998, the density of breeding kestrels was particularly low (approx. 0.1 nests per km²), and clutch and brood sizes also were smaller than in years with high density of voles (see Korpimäki 1984, Korpimäki and Wiehn 1998). Males provide females with food from the time of pair-forming to the mid-nestling period while the females incubate and brood the young. Females begin to leave the nests to hunt when the nestlings are about two weeks old (Village 1990, Tolonen and Korpimäki 1994).

Because yearling males rear smaller broods than adult males (Village 1986, Korpimäki and Wiehn 1998), nests of yearling males were excluded (only two yearling males were recorded breeding in 1998). It is easy to identify yearling males at a distance in the field because they have female-like plumage (Village et al. 1980, Village 1990, Hakkarainen et al. 1993). Boxes were checked regularly to determine the start of egg-laying, clutch size, hatching date (accurate to half a day), and the number of hatched and fledged young. Two last-hatched nestlings died on the first five days of the nestling period and the second smallest chick was chosen to represent the last-hatched one. Thereafter, no chick mortality occurred in either experimental or control nests.

Different meteorological parameters were recorded daily. During the study, mean air temperature was 18 ± 1°C, clouds were present 60% of the time and precipitation occurred on 13% of the days. Because the field season was nearly always windy, we did not take into account the wind speed (around 5–6 m/s) in our analysis.

Feeding experiments
Five nests (15 nestlings) were supplemented with food and seven others were used as controls (21 nestlings). To ensure a similar temporal distribution of food-supplemented and control nests, we used hatching date rather than laying date as the criterion for selection. Dead rooster chicks, about 30 g each, were provided to kestrel nestlings inside nest-boxes every other day from the time the first-hatched young was about 1–2

### Material and methods

#### Study area and species

The study was conducted during 1998 in the vicinity of Kauhava and Lapua, western Finland (63°N, 23°E). The main study area is a flat agricultural area broken up by small islands of trees, bushes and woods, two peatland bogs, large ditches, and two rivers. The rest of the area consists of smaller agricultural fields surrounded by coniferous forests (Korpimäki and Norrdahl 1991, Korpimäki and Rita 1996, Korpimäki and Wiehn 1998). On open agricultural land, kestrels bred in nest-boxes mounted on barns and solitary trees.
days old until the time of fledging (i.e. when the last-hatched chick of the brood was 26 days old). Kestrel broods were fed with one rooster chick per nestling during the first week of hatching, and thereafter with two rooster chicks per nestling. This corresponds to approximately half of the daily food requirement of kestrel nestlings (Masman et al. 1989). During the first two weeks of the nestling period, females fed the young with rooster chicks and sometimes hid the remaining food on the ground in the vicinity of the nest for later use. Males do not eat supplemented food provided at nest-boxes (Wiehn and Korpimäki 1997). During the last two weeks of the nestling period, kestrel chicks consumed the supplemented food on their own.

**Nestling parameters**

We used naturally asynchronous broods to compare the growth of siblings in relation to hatching order and age. Sex ratio did not differ between groups of first-, second- and last-hatched nestlings (χ2 = 0.75, df = 2, P > 0.1) nor did the mass of females and males differ (186.1 ± 2.7 vs 178.6 ± 3.03, F1,102 = 1.7, P = 0.195). Because sex was never significant as a covariate in ANCOVAs (P > 0.13), it was not included in our analysis. Sex was determined by analysing two CHD (Chromo-Helicase-DNA binding) genes (Ellegren 1996).

Growth was studied in first-, second- and last-hatched nestlings (n = 12 in each group). The difference in age was 3.0 ± 0.3 days between first- and last-hatched chicks, and 0.3 ± 0.1 days between first- and second-hatched chicks. These age differences were similar in control and supplemented nests (first- vs last-hatched chick: t-test, t11 = 1.04, P = 0.32; first- vs second-hatched chick: t11 = 0.97, P = 0.36). To evaluate the nestling growth pattern in relation to the food treatment, we used the following logistic equation (performed with Sigmaplot) fitted for control and food-supplemented broods separately:

\[ Y(x) = A_1 [1 + e^{-(x - x_0)/b}] \]

where \( Y(x) \) is the mass (g) of a chick at age \( x \) (number of days), \( A \) the asymptotic mass (g), \( b \) the growth constant (day) and \( x_0 \) the inflection point of the growth curve (day). Growth data were taken every 3–4 day.

The statistical comparison of the body mass of chicks was made at three ages: 12 days (range: 12–13; point before the mass peak), 19 days (range: 18–21; corresponding to the mass peak, Dijkstra 1988) and 26 days (range: 25–27; fledging occurs at 27–32 days, Cramp and Simmons 1980, Korpimäki and Rita 1996). To ensure similar age of first-, second- and last-hatched nestlings, all measurements of the chicks were taken on separate days. Birds were weighed to the nearest 1 g using a spring balance, most often in early morning before the first meal. When body mass was taken after 6 a.m., we checked the chick’s throat and discarded unreliable weights (i.e. when the chick had food in the crop). In addition, the lengths of wing and the sixth primary feather were taken to the nearest 1.0 mm and the length of tibiotarsus and tarsometatarsus to the nearest 0.1 mm. Univariate metrics are considered inadequate to determine the overall body size of a bird (Rising and Somers 1989, Freeman and Jackson 1990). Therefore, we used a principal component analysis (PCA) and, in particular, the first axis (PC1) of PCA. PC1 had the highest degree of correlation with the four variables (length of wing, primary, tibiotarsus and tarsometatarsus) measured and explained 84% of the total variance in nestling body size. In addition, to distinguish bone and feather growth, we determined bone size (length of tarsometatarsus and tibiotarsus; PC1b explaining 87% of the total variance in size) and feather size (length of wing and sixth primary; PC1f explaining 99.8% of the total variance in size) separately. Body mass has commonly been used to estimate the quality of individuals (i.e. the amount of body reserves (e.g. Wijnandts 1984). However, this has been criticised because both body size and body nutrients (proteins and lipids) influence the body mass of individuals (Piersma and Davidson 1991, Lindström and Piersma 1993). In addition to body mass, we used body condition of nestlings (reflecting body nutrients), which was obtained by computing residuals of a regression analysis with log body mass (to obtain homogeneity of variance) as the dependent variable and body size (derived from PC1) as the independent variable (\( y = 0.05(± 0.01) + 2.25, r^2 = 0.55, P < 0.0001, n = 104 \)).

**Body temperature and resting metabolism**

Body temperature and resting metabolism were measured for each chick (first-, second- and last-hatched chicks) at the age of 12, 19 and 26 days. After weighing, body temperature of nestlings was measured in the cloaca with a medical electronic thermometer to the nearest 0.1°C (after 30–50 s). We emphasize that resting metabolism in this study was the metabolism of growing nestlings. Resting metabolism was obtained by measuring oxygen consumption with a portable oxygen analyser (oxor II, Bucharach). Chicks were placed in a box (volume 1768 cm³) connected to the analyser. The set-up was a gas closed circuit. Because the two tubes of the analyser were at both ends of the cylindrical box, air circulated through the closed system to assure gas homogeneity in the box. The range of decrease of the oxygen fraction (ΔFO2) was 20.9 to 18.9% (we never went below the value of 18.9% to avoid hypercapnia). The three measurements taken each minute were averaged. To avoid stress, a small dark tissue covered the bird’s head. Before measurements, we waited a few
minutes and also checked that the bird did not move. Oxygen consumption was obtained by using the following relationship: \( n = \Delta PV/RT \) where \( n \) is the number of molecules of oxygen per minute and \( \Delta P \) the partial pressure (\( \Delta P = \Delta F_{O_2} \) (\( Pt - PH_{2O} \)) with \( Pt \) being the total pressure and \( PH_{2O} \), the water-vapour pressure obtained by the relation between water-vapour pressure and temperature; see Comroe 1966). \( V \) is the volume in which gas distribution is homogeneous: \( V \) was obtained by using the box volume minus the chick volume (estimated by the ratio of the mass of the chick and its density \( 0.90 \, g/cm^3 \); Sturkie 1976) and the volume of the analyzer’s tubes. \( R \) is the universal gas constant (\( 0.082 \, l \times atm/K \times mol \)), and \( T \) is the absolute temperature (\( K = 273 + T_{box} \) in Kelvin).

**Statistical analysis**

Repeated measures ANOVAs were used to test the influence of food supplements as an independent factor, and age or hatching order as factors for parameters measured on chicks. Comparisons of means between food-supplemented and control nests were performed with Student’s t-test or, when the assumption of normality failed, with the Mann-Whitney U-test. Because data on growth for the same animal or within a brood were not independent, the homogeneity of residual errors of all linear regressions was checked with the Kolmogorov-Smirnov test. Statistical analyses were performed with SPSS for Windows (Norusis 1993).

![Graph showing body mass gain of kestrel chicks from hatching to the age of 26 days.](image)

**Results**

Mean hatching dates of nests with and without food supplements were similar (16 ± 1 vs 11 ± 2 June, respectively, \( U_{2,5} = 10, p = 0.27 \), range from 6 to 21 June). Both clutch and brood size may affect fledging body mass (Wiebe et al. 1998), but there was no difference in either clutch size or brood size during the mid-nesting period between control and food-supplemented nests (mean ± se: clutch size, 5.1 ± 0.1 vs 5.0 ± 0.0, \( U_{5,7} = 13, p = 0.53 \); brood size, 4.9 ± 0.1 vs 4.6 ± 0.3, \( U_{5,7} = 15, p = 0.76 \)).

**Body mass**

Supplemented food had no obvious effect on body mass of nestlings, because the asymptotic mass, growth rate and inflection point were similar between control and food-supplemented nests (Fig. 1). In neither category did we find any obvious mass over-shoot at the age of 19 days. Because growth pattern was independent of food treatment, we pooled data to study chick growth rate. One day-old chicks weighed 21 ± 3 g. Maximum gain of mass was on the 8th day (see the inflection point value in the legend of Fig. 1). Body mass was lower on the 12th day (153 ± 3 g) than on days 19 (194 ± 3 g) and 26 (199 ± 4 g) (\( F_{1,92,62} = 123.9, p < 0.001 \)) but remained similar between days 19 and 26. This growth pattern was also found in the first-, second- and last-hatched nestlings separately (Table 1; Tukey test, \( p < 0.05 \)).

Body mass was not affected by hatching order at 12 days old (Table 2A). However, body mass of 19 days old young was lower in last-hatched nestlings than in older siblings, and was also lower in second-hatched chicks than in first-hatched ones (Table 2B; Tukey test, \( p < 0.05 \)), but these differences were no longer detectable at the age of 26 days (Table 2C).

**Body size**

In contrast to body mass, body size increased from hatching to fledging (26th day) in the first-, second- and last-hatched nestlings (Table 1). At the age of 12 days, the food supplement but not hatching order had an effect on body size, which was smaller in control than in food-supplemented chicks (Table 2A). This effect is linked to the fact that first- and second-hatched chicks were smaller in control than food-supplemented nests (significant interactions in Table 1A and B; Tukey test, \( p < 0.05 \)). This effect was particularly marked for feather length (\( F_{1,9,17.1} = 307.1 \) and \( F_{1,7,16} = 62.3 \) in first- and second-hatched nestlings, respectively, \( p < 0.01 \)). At the age of 19 days, body size was related to hatching order (Table 2B) with last-hatched chicks...
Table 1. The effect of age (days 12, 19 and 26) and treatment (food supplement or control) on body mass, size and condition of kestrel chicks according to hatching order (first-, second- and last-hatched). Repeated measures ANOVA.

<table>
<thead>
<tr>
<th>Hatching order</th>
<th>Body mass</th>
<th>Body size</th>
<th>Body condition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>A) First-hatched</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age (A)</td>
<td>2</td>
<td>53.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Treatment (T)</td>
<td>1</td>
<td>0.12</td>
<td>0.738</td>
</tr>
<tr>
<td>A × T</td>
<td>2</td>
<td>0.55</td>
<td>0.588</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>B) Second-hatched</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age (A)</td>
<td>2</td>
<td>65.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Treatment (T)</td>
<td>1</td>
<td>0.02</td>
<td>0.877</td>
</tr>
<tr>
<td>A × T</td>
<td>2</td>
<td>0.58</td>
<td>0.572</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td>11.5</td>
<td>18</td>
</tr>
<tr>
<td>C) Last-hatched</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age (A)</td>
<td>2</td>
<td>19.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Treatment (T)</td>
<td>1</td>
<td>3.85</td>
<td>0.085</td>
</tr>
<tr>
<td>A × T</td>
<td>2</td>
<td>0.12</td>
<td>0.889</td>
</tr>
<tr>
<td>Error</td>
<td>16</td>
<td>16</td>
<td>16</td>
</tr>
</tbody>
</table>

* When the data do not meet the sphericity assumption, the degrees of freedom are corrected by the epsilon of Huynh-Feldt.

Table 2. The effect of hatching order (first-, second- and last-hatched chicks) and treatment (food supplement or control) on body mass, size and condition of kestrel chicks at the age of 12, 19 and 26 days. Repeated measures ANOVA.

<table>
<thead>
<tr>
<th>Age (days)</th>
<th>Body mass</th>
<th>Body size</th>
<th>Body condition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>A) 12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hat. order (H)</td>
<td>1.6</td>
<td>0.07</td>
<td>0.901</td>
</tr>
<tr>
<td>Treatment (T)</td>
<td>1</td>
<td>1.17</td>
<td>0.307</td>
</tr>
<tr>
<td>H × T</td>
<td>1.6</td>
<td>1.22</td>
<td>0.314</td>
</tr>
<tr>
<td>Error</td>
<td>14.4</td>
<td>12.2</td>
<td>15.9</td>
</tr>
<tr>
<td>B) 19</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hat. order (H)</td>
<td>1.5</td>
<td>16.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Treatment (T)</td>
<td>1</td>
<td>0.84</td>
<td>0.381</td>
</tr>
<tr>
<td>H × T</td>
<td>1.5</td>
<td>1.93</td>
<td>0.183</td>
</tr>
<tr>
<td>Error</td>
<td>15.5</td>
<td>14.9</td>
<td>20</td>
</tr>
<tr>
<td>C) 26</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hat. order (H)</td>
<td>1.5</td>
<td>3.63</td>
<td>0.065</td>
</tr>
<tr>
<td>Treatment (T)</td>
<td>1</td>
<td>0.03</td>
<td>0.869</td>
</tr>
<tr>
<td>H × T</td>
<td>1.5</td>
<td>3.55</td>
<td>0.068</td>
</tr>
<tr>
<td>Error</td>
<td>13.5</td>
<td>13.3</td>
<td>15.4</td>
</tr>
</tbody>
</table>

The present data do not meet the sphericity assumption (except for body condition on the 19th day). The degrees of freedom are corrected by the epsilon of Huynh-Feldt.

being smaller than first-hatched ones (Tukey test, P < 0.05, see Fig. 2A). Just before fledging (26th day), the effect of hatching order on body size was no longer detectable (Table 2C; Fig. 2A), the last-hatched chick having achieved the same bone and feather lengths as older siblings (F2,17.1 = 0.13, P = 0.87; F2,10.8 = 0.89, P = 0.39, respectively).

**Body condition**

Body condition of the first- and last-hatched chicks did not change markedly over the growth period (Table 1; Fig. 2B). Only body condition of second-hatched chicks was higher at the age of 19 than at the age of 26 days (Tukey test, P < 0.05). Body condition was affected by hatching order when chicks were 19 and 26 days old (Table 2B, C). When 19 days old, last-hatched nestlings had a lower body condition than other chicks (Fig. 2B; Tukey test, P < 0.05). In contrast to body mass, body condition at 26 days differed according to hatching order (the standard error was lower for body condition than for body mass). When nestlings were 26 days old, body condition in control nests was lower in the last-hatched chick than in its siblings, whereas body condition in food-supplemented nests did not differ between chicks (significant interaction in Table 2C and Fig. 2B; Tukey test, P < 0.05).
Body temperature

Body temperature was strongly related to air temperature (y = 0.14( ± 0.01)x + 36.99, r² = 0.49, P < 0.001, n = 104). To remove the effect of air temperature, we used residuals from the regression analyses (residuals were homogeneous, Kolmogorov-Smirnov test, P > 0.05). Residuals of body temperature varied as a function of nestling age. Twelve-day old chicks had a lower body temperature than 26-day old chicks independent of hatching order (ANOVA with repeated measures: first-hatched chick: F2,16 = 11.2, P = 0.001; second-hatched chick: F2,11.5 = 9.2, P < 0.01; last-hatched chick: F2,16 = 6.1, P < 0.05). For a given age, body temperature was not associated with hatching order (ANOVA with repeated measures, P > 0.1). Food treatment and interactions between age and food treatment or between hatching order and food treatment were not significant (P > 0.4). Body temperature was positively correlated with body mass and body condition (ANCOVA: F1.98 = 57.1, P < 0.001; F1.98 = 6.84, P = 0.01; hatching order-covariate interactions, P > 0.1).

Resting metabolism

Oxygen consumption (l/bird/day) varied with air temperature (y = −0.12( ± 0.04)x + 10.57, r² = 0.10, P = 0.001, n = 101). Because we were interested in resting metabolism, we used residuals from the regression analysis to remove the effect of air temperature (residuals were homogeneous, Kolmogorov-Smirnov test, P > 0.05). Resting metabolism (residuals of oxygen consumption) was related to nestling age, being lower at the age of 12 than at 26 days old in both first-(ANOVA with repeated measures, F2,16 = 5.5, P < 0.05) and last-hatched (F2,16 = 4.9, P < 0.05) chicks. Resting metabolism was also associated with hatching order. As found for body mass (see above), the last-hatched chick at the age of 19 days had lower resting metabolism than the other chicks (Fig. 3). When chicks were 26 days old, resting metabolism was independent of hatching order (Fig. 3). Food treatment and interactions between age and food treatment or between hatching order and food treatment were not significant (P > 0.2). ANCOVA with repeated measures (hatching order as independent factor) showed that resting metabolism was positively correlated with covariates such as body mass, body condition and body temperature (F1.98 = 33.7, P < 0.001; F1.96 = 8.1, P < 0.01; F1.96 = 21.1, P < 0.001; hatching order-covariate interactions, P > 0.1).
Discussion

These results from wild kestrels show that hatching order delays growth and resting metabolism of the last-hatched chick relative to older siblings until one week before fledging. At fledging, however, the youngest chick had caught up with older siblings in body mass, body size and resting metabolism, whereas its body condition attained the level of older siblings only in food-supplemented nests, not in control nests.

Growth of nestlings

The bell-shaped curve of postnatal growth, reflecting fat deposition in house martins Delichon urbica (Bryant and Gardiner 1979) or water accumulation in barn owls Tyto alba (Durant 2000), can be observed in several species of birds, including the kestrel (Korpimäki et al. 1979, Kuusela and Solonen 1984, Kostrzewa and Kostrzewa 1987, Dijkstra 1988). No over-shoot in mass was found in either control or food-supplemented chicks in our study. When 19 days old, nestlings had almost attained fledging mass. Because the peak in chick mass has been shown to reflect a high food intake, we suppose that the lack of mass over-shoot was due to food deprivation. Indeed, the density of the main food (voles) during the study year was extremely low. Why did not nestlings in food-supplemented nests show a bell-shaped curve in postnatal growth? Parent females in food-supplemented nests are heavier and also decrease their parental effort (Wiehn and Korpimäki 1997). Therefore, females seem to benefit more from food supplementation than their brood because females eat some of the supplemented food and decrease their hunting activity. Similar fledging masses of food-supplemented and control broods were also found by Wiehn and Korpimäki (1997). As also found in house sparrows Passer domesticus (Lepczyk and Karasov 2000), growth rate in our study was not modified by changes in food availability. Taken together, these data suggest that extra food did not markedly improve the quality of nestlings even in low food abundance conditions.

Wiehn and Korpimäki (1997) showed that fledging mass of kestrel chicks was lower in years of low than in years of high vole abundance. Fledging mass in our study was similar to that in low food years. Body mass of chicks had already reached fledging mass at the age of 19 days but why did the mass gain stop already at this age, about one week before fledging? We suppose that the prey delivery rate in the very poor food year was not high enough to increase mass in either control or food supplemented chicks. This is supported by the fact that their body condition did not differ between days 19 and 26 (except in second-hatched nestlings), indicating that the relative proportion of body reserves was not modified during that part of the nestling period.

The body size of kestrel nestlings increased continuously during the mass growth, as reflected by the increases in both bone and feather lengths. When nestlings were 12 days old, feathers were shorter in control chicks than in food-supplemented chicks, while bones had similar lengths. These data are in accordance with the fact that bone length appears to be more strongly determined by genetic factors and, therefore, is less susceptible to environmental variability (Gard and Bird 1992), whereas feather development is more strongly influenced by malnutrition (Negro et al. 1994, Lacombe et al. 1994).

Body temperature and resting metabolism gave us some information about the muscle maturity of nestlings. Both body temperature and resting metabolism were low in kestrel nestlings at the age of 12 days and increased until 26 days after hatching. The capacity to thermoregulate and the functional maturity of skeletal muscle are negatively correlated with fast growth (Ricklefs 1979, Kirkwood 1981). In kestrel nestlings, the maximum mass gain (inflection point of growth curve) occurred at 8 days old. Thus, muscle maturation at this stage probably does not allow a sufficient muscle thermogenesis to maintain a body temperature similar to that found after the age of 12 days. The low body temperature at the age of 12 days could also be related to a poor plumage development, primary feathers erupting from quills only after this age (Village 1990, pers. obs.).

Hatching order and growth

In accordance with our prediction, the delayed growth in body mass and size in last-hatched young at the age of 19 days had disappeared at 26 days both in nests with and in nests without food supplements. The last-hatched nestlings thus seem to grow until the age of 26 days, so that their body mass and size were similar to those of their siblings in which growth levelled off when they were 19 days old. Our study was performed under unfavourable environmental conditions (low abundance of natural food, and unusually low summer temperatures and much rain). These conditions may limit hunting time (Tolonen and Korpimäki 1994), prey delivery (Cavé 1968, Dijkstra 1988, Tolonen and Korpimäki 1994) and nestling growth (black kite Milvus migrans, Hiraldo et al. 1990, pied flycatcher Ficedula hypoleuca, Siikamäki 1996). However, kestrel nestlings seem to compensate partly for the delay in body mass and size gain, suggesting a growth flexibility. In fact, growth flexibility is characteristic of some species. Chicks of the common swift Apus apus interrupt development and can survive long periods of food restriction (Ricklefs 1983), whereas some passerine species are unable to
delay growth, thereby threatening the survival of chicks (O’Connor 1984, Konarzewski et al. 1996). Kestrels seem to fall between these two extremes, because no long-term effect of food deprivation on growth was found in our study nor in a study of the American kestrel (Negro et al. 1994), suggesting the existence of an adaptive mechanism permitting compensation for day-to-day fluctuations in food supply.

However, there are limits to the flexibility of this growth pattern. In contrast to our prediction, the poorer body condition of last-hatched young found at 19 days was still present one week later in control nests but not in food-supplemented nests. It is important to know if the decrease in body condition reflects a loss of lipid or protein at that time. We show in this study that body condition is correlated with resting metabolism. Resting metabolism, which depends on the energy expenditure of several tissues, including heart, kidney, brain, liver and skeletal muscle, is proportional to the muscle mass of an individual (Schmidt-Nielsen 1979, Daan et al. 1989, Scott and Evans 1992, Scott et al. 1996, Visser 1998). Compared to the other 19-day-old chicks, the lower resting metabolism of the last-hatched chick at this age therefore suggests a smaller muscle mass. Because resting metabolism just before fledging was similar regardless of hatching order, the last-hatched chicks seemed to have caught up with respect to muscle mass. At that time, however, body condition of last-hatched chicks was poorer than that of the other chicks in control nests, probably reflecting smaller lipid stores in these subdominant chicks. As previously hypothesized (Lacombe et al. 1994), a last-hatched nestling suffering from food restriction may therefore be unable to store as much fat as older siblings. In summary, despite a flexible growth in body mass and size, hatching order affects the body condition of last-hatched fledglings.

The poorer nutritional state of last-hatched fledglings may lead to a higher post-fledging mortality, because fledgling quality is correlated with future survival in several species of birds (e.g. Perrins 1965, Thompson 1971, Perrins et al. 1973, Murphy 1978, Korpimäki 1988, Magrath 1989, 1991, Tinbergen and Boerlijst 1971, Perrins et al. 1973, Murphy 1978, Korpimäki 1990, Brinkhof et al. 1997). In kestrels (Negro et al. 1994), suggesting that there is still sibling competition for food. In conclusion, the growth flexibility of nestling Eurasian kestrels may allow them to reduce the effects of starvation, in particular the starvation to death of last-hatched chicks. Nonetheless, food restriction imposed by sibling competition within asynchronous broods can affect the level of lipid stores at fledging.

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