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Maternal compensation for hatching asynchrony in the collared flycatcher *Ficedula albicollis*

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Several hypotheses have been proposed to explain the adaptiveness of hatching asynchrony for the parents, but delayed hatching is generally detrimental for the late hatched young. These offspring often experience competitive disadvantage and delayed development. If hatching asynchrony has a reason other than producing competitive differences among offspring, it would be advantageous, not only for the offspring but even for the parents, to compensate for its detrimental effects. In some species, increasing investment into later laid eggs has been reported and discussed as a compensation mechanism, but its effect on nestling growth and fledging size has not been examined in details. In this study we investigated nestling growth and size at fledging in terms of body mass and length of primaries in relation to the accurate laying and hatching order in collared flycatcher *Ficedula albicollis* broods. We found that females laid larger eggs at the end of the laying sequence, and this helped to decrease the disadvantages for the last offspring. The last offspring had lower body mass growth rate and fledged with shorter feathers, but in both cases the larger the last egg was, the smaller the lag of the offspring was. We conclude, that even if females were not able to fully compensate for the detrimental effects of hatching asynchrony, larger eggs may improve the survival prospects of late hatched nestlings.

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In many bird species females start to incubate their eggs before the whole clutch has been laid, thus the last laid eggs hatch asynchronously. Hatching asynchrony (HA) may provide various benefits to the parent birds (Stenning 1996). For example, by starting to incubate their clutches before completion, females can reduce predation risk to their brood, because some of their offspring start to develop and fledge earlier, so the average time spent in the nest will be shorter (nest failure hypothesis, Hussell 1972). Moreover, earlier onset of incubation may also result in higher hatching success, because the viability of eggs, if they are not incubated, declines with time (egg viability hypothesis, Arnold et al. 1987, Veiga 1992).

The brood reduction hypothesis (Ricklefs 1965, Lack 1968, Forbes et al. 1997) links parental benefit from HA to environmental unpredictability. According to this hy-

pothesis, the last hatched offspring is a surplus that may die if the food is scarce, but confers extra benefit to their parents if the food is abundant. For further hypotheses on HA see e.g. Nilsson (1993) and Stenning (1996).

For the last offspring, these hypotheses predict reduced survival probability (Oddie 2000), because delayed hatching results in competitive disadvantage (Price and Ydenberg 1995, Ostreiher 1996) and reduced fledging weight (Cotton et al. 1999, Clotfelter et al. 2003). If the brood reduction hypothesis is true, parents have no interest in compensating for this disadvantage, while in case of the egg viability and nest failure hypotheses, parents benefit from compensation. The most obvious way to achieve such a compensation is preferential feeding of the later hatched offspring by one or both of the parents (Gottlander 1987). However, compensation may also act through preferential

maternal investment into the later laid eggs (Howe 1976, Schwabl 1993, Schwabl 1996, Cichoń 1997, Lipar and Ketterson 2000, Eising et al. 2001). This differential investment may be manifested in an elevated level of testosterone to increase the competitive ability (Schwabl 1993, Lipar and Ketterson 2000) and the development of nestlings (Schwabl 1996, Eising et al. 2001). Females may enhance the survival prospects of their nestlings also through preferential nutrient investment into the eggs (Howe 1976, Cichoń 1997, Royle et al. 1999, Reynolds et al. 2003). On the other hand, species with a brood reduction strategy may reduce the investment into the last laid eggs (testosterone: Schwabl et al. 1997; nutrients: Arnold 1989, Heeb 1994, Viñuela 1997), thereby exaggerating the competitive disadvantage of the surplus offspring.

Egg size is known to correlate with the nutrient investment. Several studies have reported that egg size reflected the lipid and/or protein content of the eggs (Meathrel and Ryder 1987, Williams 1994, Hill et al. 1995, Royle et al. 1999, Jager et al. 2000, Badzinski et al. 2002, Reynolds et al. 2003), providing an indirect measure of maternal favouritism through egg nutrients.

In our study we investigated whether collared flycatcher *Ficedula albicollis* females compensated for or aggravated the disadvantageous effect of HA on the later hatched nestlings. In this species, parents do not discriminate between nestlings of different size when they allocate food (Rosivall et al. 2005), thus parental compensation for HA is possible only during the egg-laying period. To assess nutrient investment into the eggs and its effect on nestling development, we measured egg size and nestling growth. Some earlier studies have already attempted to investigate the effect of laying order on the growth and fledgling condition of nestling passerines, but very few studies linked the growth of individual nestlings to the exact laying and hatching order (Badyaev et al. 2002), and these studies did not focus on possible maternal compensation for the detrimental effects of HA.

Methods

Study species and field methods

This study was conducted in an artificial nest box plot in the Pilis Mountains, Hungary (47°43′N, 19°01′E) in 2002 and 2003. The study plot is a part of a continuous, unmanaged, oak-dominated woodland, a protected area of Duna-Ipoly National Park. For a more detailed description of the study site see Török and Tóth (1988). The collared flycatcher is a small hole-nesting, long-distance migratory passerine bird. The breeding season starts in mid April. Females usually lay 5–7 eggs. The eggs hatch approximately 12 days after the last egg was laid. Nestlings usually fledge 14–15 days after hatching.

We studied altogether 45 broods (22 in 2002 and 23 in 2003). In order to exclude possible confounding seasonal effects on egg size and nestling growth, these broods were selected so that the first egg was laid within a 6 and 4 day interval (in 2002 and 2003, respectively). All eggs were numbered with a permanent marker on the day of laying. The length and breadth of eggs were measured to the nearest 0.1 mm using a calliper. All clutches were placed into an incubator (PL Machine SK75) one day before the expected hatching date and replaced with dummy eggs of approximately equal size. All females accepted these dummy eggs as their own and continued the incubation. The original eggs were hatched in separated compartments at 37.2°C and 70–80% humidity. All embryos, which were still alive when placed into the incubator, hatched successfully. We checked hatching every hour from 4:15 am to 9:00 pm. For eggs hatching during the night we assumed that they hatched halfway between the last and the first checking.

Each hatchling was weighed to the nearest 0.01 g with an electronic balance (Mettler PM4800), marked individually on their breast with a permanent non-toxic pen and returned to their nest immediately, or early the following morning if they hatched during the night. Colour marking was randomized in relation to hatching order. We followed body mass increase of the nestlings in all broods from the day when the first chick(s) in a brood hatched (day 0) and the growth of the wing feathers in 34 broods from day 8 until fledging. Body mass and the length of the third outer primary were measured every second day to the nearest 0.1 g and 0.5 mm respectively. On day 14, body mass was measured in all broods, and the length of the third outer primary was measued in all but one brood.

Data analysis

In this study we used 45 clutches consisting of 6 or 7 eggs. Because it may be different being laid sixth in a clutch of 6 or 7 eggs, we ranked each egg into one of the following five categories: first, second, middles, penultimate and last laid egg. See e.g. Magrath et al. (2003) for a similar grouping.

Egg volume (V) was calculated according to the formula $V = -0.042 + 0.4976 \times L \times W^2$, where $L =$ egg length and $W =$ egg width, described by Ojanen et al. (1978) for a sibling species, the pied flycatcher *Ficedula hypoleuca*. Place of a chick in the hatching order was described by the hatching time, which was calculated as the time elapsed between the first hatching in a brood and the hatching of the chick in question. Hatching time was therefore 0.0 h for the chicks hatched first in a brood. Mass was found to increase logistically with time, so we calculated the rate of mass increase (K) for each individual using the following logistic growth model:

$W = A/(1 + \exp(-K \times (t - t_i)))$ (Starck and Ricklefs 1998) where t was the accurate age of the focal individual, calculated from the hatching time. The growth of the primaries was linear so we used the slope of a linear regression to describe feather growth rate (Nilsson and Svensson 1996) and we did not control for the accurate hatching time.

Unless stated otherwise, analyses were performed using general linear mixed models with laying order as repeated measure factor and year and brood size as factors. The covariance structure of the model was selected on the basis of Schwarz's Bayesian Information Criterion (Littell et al. 1996). For all but one of the dependent variables the best fit was achieved by using first order autoregressive covariance, therefore we used this covariance structure throughout the analyses. This covariance structure assumes that measurements closer in the repeated measure sequence are more similar to each other, which is our expectation if eggs are laid sequentially. Denominator degrees of freedoms are obtained by Satterthwaite approximation and are therefore not integers. Post hoc comparisons were performed contrasting the groups in question in the Test Subcommand of the SPSS. Statistical analyses were performed using SPSS 11.0 and Statistica for Windows 4.5.

Sample sizes varied among dependent variables. Five broods (2 and 3 in 2002 and 2003, respectively) were not included in the nestling growth analyses, because females reared their young alone. Inclusion of these broods in the investigation of egg size patterns did not change the result, therefore they were kept in this analysis. Feather growth was measure in 34 broods only, therefore this analysis based on a smaller dataset. Because of unhatched, died or not measured nestlings some data were occasionally missing. However, hatching success and subsequent nestling survival (95.8% and 98.8%, respectively) were not related to laying order (χ^2-test were used to compare the distribution of hatched/survived chicks to the number of observations throughout the laying order; hatching success: $\chi^2 = 0.615$, df $= 4$, P $= 0.961$; survival: $\chi^2 = 0.080$, df $= 4$, P $= 0.999$) and therefore they are not expected to affect the outcome of our analyses.

Results

We found that in collared flycatcher clutches, egg volume increased with laying order (Table 1, Fig. 1). Hatching mass showed a similar increase (Table 1), and it was the consequence of increasing egg volume, because when the residuals of hatching mass on egg volume were entered into the mixed model, laying order was no longer significant (F $= 0.40$, df $= 4$, P $= 0.81$).

The significant overall effect of laying order on hatching time indicates that broods hatched asynchronously, but there was a difference between the two study

Table 1. The effect of laying order (first, second, middle, penultimate, last), brood size (6, 7) and study year (2002, 2003) on egg volume, hatching time (time since the first nestling in the focal brood hatched), nestling growth (K of the logistic mass growth curve and the slope of the linear feather growth) and fledgling size (body mass and length of the third outer primary on day 14). Displayed are F values with degrees of freedom in parentheses. Asterisks indicate the level of significance (*P < 0.05, **P < 0.01, ***P < 0.005).

|	Egg volume	Hatching mass	Hatching time	Mass growth	Feather growth	14 d mass	14 d feather
Brood size	1.06 (1, 41.90)	1.17 (1, 36.19)	10.76 (1, 51.43)***	0.25 (1, 43.15)	0.02 (1, 34.63)	0.05 (1, 40.83)	0.03 (1, 38.81)
Year	1.02 (1, 41.90)	0.03 (1, 36.19)	2.35 (1, 51.43)	0.23 (1, 43.15)	0.33 (1, 34.63)	0.99 (1, 40.83)	22.99 (1, 38.81)***
Laying order	15.65 (4, 154.69)***	5.14 (4, 123.08)***	135.13 (4, 114.13)***	7.55 (4, 121.07)***	1.52 (4, 88.90)	0.24 (4, 124.35)	15.71 (4, 111.24)***
Brood size × year	1.29 (1, 41.90)	2.29 (1, 36.19)	0.64 (1, 51.43)	1.31 (1, 43.15)	0.17 (1, 34.63)	2.32 (1, 40.83)	1.82 (1, 38.81)
Brood size × laying order	1.08 (4, 154.69)	0.34 (4, 123.08)	1.85 (4, 114.13)	1.30 (4, 121.07)	1.68 (4, 88.90)	0.75 (4, 124.35)	1.62 (4, 111.24)
Year × laying order	1.18 (4, 154.69)	0.28 (4, 123.08)	2.02 (4, 114.13)	2.27 (4, 121.07)	0.62 (4, 88.90)	1.40 (4, 124.35)	0.33 (4, 111.24)
Brood size × year × laying order	0.68 (4, 154.69)	0.87 (4, 123.08)	2.49 (4, 114.13)*	0.72 (4, 121.07)	3.27 (4, 88.90)*	0.22 (4, 124.35)	0.18 (4, 111.24)
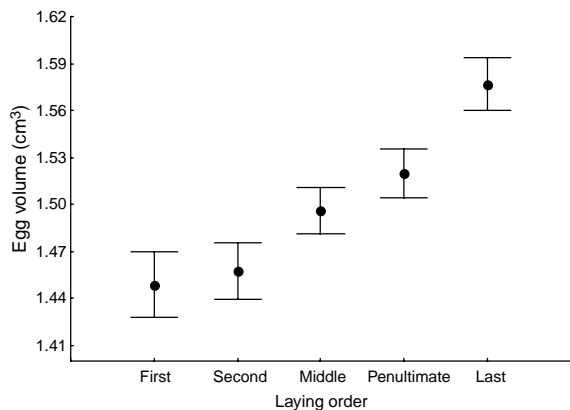
Fig. 1. Egg volume (mean±SE) in relation to laying order in collared flycatcher broods.

years (Table 1, Fig. 2). In 2002 the last egg hatched later in clutches with 6 eggs (P <0.001), while the last two in clutches with 7 eggs (both for last-earlier laid and
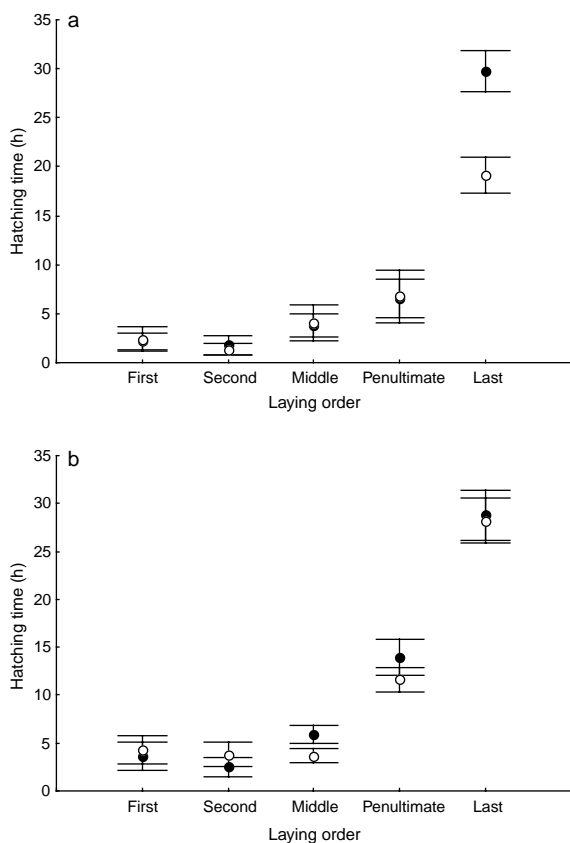

Fig. 2. Hatching time (mean±SE) in relation to laying order in collared flycatcher broods of six (a) and seven (b) eggs. Hatching time is the time elapsed between the first hatching in a brood and the hatching of the chick in question. Hatching time was therefore 0.0 h for the chicks that hatched first in a brood. Open circles: 2002; filled circles: 2003.

penultimate-earlier laid comparison P <0.001). In 2003 the last two eggs hatched later independent of the brood size (all P <0.007). When we entered the hatching asynchrony (the time difference between the first and last hatching) to an ANOVA with brood size and year as factors, the overall year effect was significant (F =5.62, df =1, 33, P =0.024). In 2003 hatching asynchrony was more pronounced (mean±SE was 25.20±1.78 and 29.50±1.65 in 2002 and 2003, respectively). The difference was more pronounced for the 6-egg clutches (year × brood size: F =4.12 df =1, 33, P =0.051).

Though the laying order × brood size × year interaction was significant, there was no overall effect of laying order on the growth of primaries (Table 1). However, laying order affected the mass increase of the nestlings (Table 1, Fig. 3). Nestlings hatched from last laid eggs experienced lower growth rate (K). In spite of the lower mass increase, there was no relationship between laying order and body mass before fledging (day 14; see Table 1). However, the primaries of the chicks hatched from the last egg were shorter than those of their nestmates (Table 1, Fig. 4). These results were consistent across years, even though in 2003 the length of the primaries was overall significantly shorter than in 2002.

The compensatory effect of larger last egg, can be tested by correlating the relative egg size of the last chicks (compared to their sibs) with their relative growth rate or fledging size. In the case of fledging mass, correlation with relative egg size is not expected, because in our broods, most chicks reached their maximal body mass on day 14 at the latest. However, the advantage of larger egg size was apparent, when we analysed its effect on body mass growth, while controlling for the effect of hatching asynchrony. In a multiple regression, relative hatching time (i.e. the difference between the hatching time of the last chick and the mean of its siblings) negatively affected the relative body mass growth rate
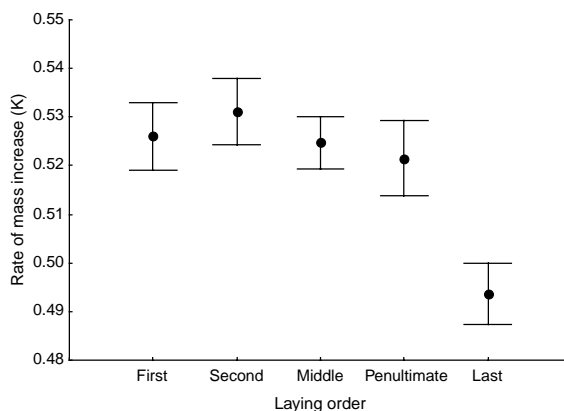

Fig. 3. Mass growth in relation to laying order in collared flycatcher broods. K is the growth rate from the logistic growth function $W = A/(1 + \exp(-K \times (t - t_i)))$, means±SE are shown.
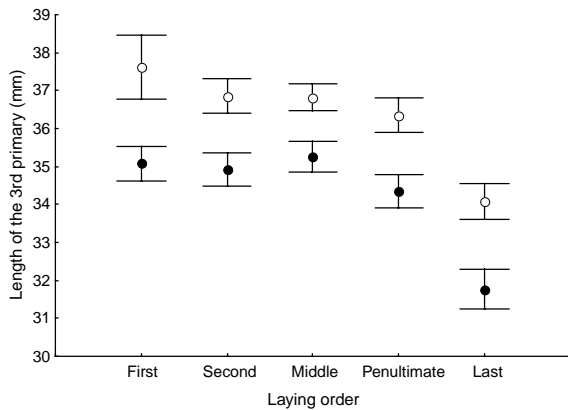
Fig. 4. Length of the third primary (mean ± SE) before fledging (14 d) in relation to laying order in collared flycatcher broods. Open circles: 2002; filled circles: 2003.

of the last chick (ß = −0.37, F = 6.11, df = 1, 32, P = 0.019), while relative egg size had a significant positive effect (ß = 0.37, F = 6.19, df = 1, 32, P = 0.018). Relative egg size also tended to affect the feather growth rate (ß = 0.35, F = 3.58, df = 1, 27, P = 0.069), though it was not affected by the relative hatching time (F = 1.14, df = 1, 27, P = 0.29). Finally, the lag of the last chick before fledging, in terms of feather length, was affected by both relative hatching time (ß = −0.41, F = 7.68, df = 1, 32, P = 0.009) and relative egg size (ß = 0.32, F = 4.73, df = 1, 32, P = 0.037). The later the nestling hatched compared to its siblings, the larger its disadvantage was, while this disadvantage was decreasing with increasing egg size.

Discussion

Here we aimed to investigate whether collared flycatchers compensate for, or magnify the detrimental effects of hatching asynchrony (HA) on the last hatched offspring by egg size differences. From this viewpoint, hypotheses concerning HA (reviewed in Stenning 1996) can be divided into two groups. Some of them (e.g. brood reduction hypothesis, sibling rivalry hypothesis) assume that parents start to incubate before clutch completion in order to aggravate the competitive differences among nestlings (Lack 1968), while others (e.g. nest failure hypothesis, egg viability hypothesis) assume that competitive differences are only the cost of the earlier onset of incubation which is adaptive for other reasons than sibling size asymmetry (Hussell 1972, Clark and Wilson 1981, Arnold et al. 1987, Veiga 1992). If females start to incubate before the clutch is complete to enhance the competitive differences, they are not expected to compensate for the disadvantage of the last chick, they may even reduce the investment into the later laid eggs (Heeb 1994, Schwabl et al. 1997, Viñuela 1997). In other cases

compensation for the disadvantage of the last hatched chick may increase the fitness of the females. In species with no conspicuous physical competition among nestlings, but with pronounced HA, most hypotheses predict that establishing competitive differences and reducing investment into later laid eggs has probably no adaptive value (but see insurance egg hypothesis, Clifford and Anderson 2001). Indeed, in collared flycatchers where there is no direct aggression between the nestlings (pers. obs.), we found that females increase the egg size with laying order, thus probably providing nutritional help for the later hatching young.

Some previous studies have also found similar egg size increase in relation to laying order (Howe 1976, Cichoń 1997) and hypothesized that it might adaptively reduce the detrimental effects of HA. In this paper, we investigated the growth and fledging size of individual nestlings. We found, that body mass before fledging was not related to laying order, which might be the effect of the logistic nature of the growth curve (i.e. older siblings finished their growth a few days before fledging, thus the last chicks had time to catch up), or the joint effect of logistic mass growth and larger last eggs. The fact that independent of the relative egg size most of the last chicks reached their maximum body mass on day 14 at the latest, might indicate that larger egg size is not needed to reach the same size as their older siblings, but it is hard to draw conclusions, because we do not exactly know how they would have grown if they had hatched from smaller eggs. However, nestlings from last laid eggs experienced slower body mass growth, and had shorter primaries before fledging than their siblings. These disadvantages were increasing with increasing HA, but were partially counterbalanced by the larger egg size. The growth of the primaries was not related to laying order, probably because synchronized fledging is important for the survival prospects of the nestlings, and therefore, they allocate more energy into growing their wing feathers at the cost of lower body mass increase (Nilsson and Svensson 1996, Nilsson and Gårdmark 2001). Still relative size of the last egg tended to correlate positively with the relative feather growth rate of the last chicks.

Reduced growth or bad body condition early in the life was reported to have negative impact, for example, on immune responsiveness, intensity of parasite infection, adult condition, time of sexual maturation and long-term survival in vertebrates, even if they could catch up later in size (Birkhead et al. 1999, Morgan and Metcalfe 2001, Blount et al. 2003, Stjernman et al. 2004). Late or asynchronous fledging due to shorter feathers, may also be disadvantageous. For instance, parents preferentially fed fledged chicks if fledglings and nestlings were begging simultaneously in the great tit *Parus major* (Lemel 1989). Thus, we argue that even the partial compensation for these adverse effects of HA by laying

larger final eggs, probably increased the survival prospects of the last chicks and thus the fitness of the parents. Though maternal compensation is possible not only through egg size, which is known to correlate with the amount of macronutrients, but also through bio-molecules (Schwabl 1993, Lipar and Ketterson 2000, Eising et al. 2001), no preferential testosterone investment in relation to laying order has been found in this species (Michl et al. 2005).

The HA and nestling development patterns within broods were consistent across years in collared flycatchers. The only difference between the two subsequent years was that HA was higher and penultimate eggs hatched relatively later in 2003 (Fig. 2), which probably means that in this year females started to incubate their broods earlier. This phenomenon is presumably the consequence of the higher mean temperature in 2003. The daily maximum temperature exceeded 25°C some days and 20°C every day during the egg-laying period of the studied broods (Török et al. unpubl. data). Such temperatures may cause lower egg viability if eggs are not incubated (von Schalkwyk et al. 1999, Viñuela 2000, Sahan et al. 2003). Thus it may explain why females started to incubate relatively earlier in this year. Alternatively, higher mean temperatures may result in better food supply, which may cause increased HA (Nilsson 1993).

In conclusion, we found that last hatched nestlings experienced slower body mass growth, and fledged with shorter wing feathers than their older siblings, but both were partially compensated by larger last eggs. Since relatively larger wing feathers may minimize the flying ability handicap of the late-hatched nestlings after fledging, and relatively faster growth early in life may increase the survival prospects of these chicks, the increase of egg size with laying order may increase the probability that all nestlings from the focal brood survive. Thus the observed egg size pattern is beneficial for both the last chick and the parents.

References

Arnold, T. W. 1989. Variation in size and composition of horned and pied-billed grebe eggs. – Condor 91: 987–989.

Arnold, T. W., Rohwer, F. C. and Armstrong, T. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. – Am. Nat. 130: 643–653.

Badyaev, A. V., Hill, G. E., Beck, M. L., Dervan, A. A., Duckworth, R. A., McGraw, K. J., Nolan, P. M. and Whittingham, L. A. 2002. Sex-biased hatching order and adaptive population divergence in a passerine bird. – Science 295: 316–318.

Badzinski, S. S., Ankney, C. D., Leafloor, J. O. and Abraham, K. F. 2002. Egg size as a predictor of nutrient composition of eggs and neonates of Canada geese (*Branta canadensis interior*) and lesser snow geese (*Chen caerulescens caerulescens*). – Can. J. Zool. 80: 333–341.

Birkhead, T. R., Fletcher, F. and Pellatt, E. J. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. – Proc. R. Soc. B 266: 385–390.

Blount, J. D., Metcalfe, N. B., Arnold, K. E., Surai, P. F., Devevey, G. L. and Monaghan, P. 2003. Neonatal nutrition, adult antioxidant defences and sexual attractiveness in the zebra finch. – Proc. R. Soc. B 270: 1691–1696.

Cichoń, M. 1997. Egg weight variation in collared flycatcher *Ficedula albicollis*. – Ornis Fenn. 74: 141–147.

Clark, A. B. and Wilson, D. S. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction and nest failure. – Q. Rev. Biol. 56: 253–277.

Clifford, L. D. and Anderson, D. J. 2001. Experimental demonstration of the insurance value of extra eggs in an obligately siblicidal seabird. – Behav. Ecol. 12: 340–347.

Clotfelter, E. D., Whittingham, L. A. and Dunn, P. O. 2003. Laying order, hatching asynchrony and nestling body mass in tree swallows *Tachycineta bicolor*. – J. Avian Biol. 31: 329–334.

Cotton, P. A., Wright, J. and Kacelnik, A. 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. – Am. Nat. 153: 412–420.

Eising, C. M., Eikenaar, C., Schwabl, H. and Groothuis, T. 2001. Maternal androgens in black-headed gull (*Larus ridibundus*) eggs: consequences for chick development. – Proc. R. Soc. B 268: 839–846.

Forbes, S., Thornton, S., Glossey, B., Forbes, M. and Buckley, N. J. 1997. Why parent birds play favourites. – Nature 390: 351–352.

Gottlander, K. 1987. Parental feeding behaviour and sibling competition in the pied flycatcher *Ficedula hypoleuca*. – Ornis Scand. 18: 269–276.

Heeb, P. 1994. Intraclutch egg-mass variation and hatching asynchrony in the jackdaw *Corvus monedula*. – Ardea 82: 287–297.

Hill, W. L., Browne, M. and Hardenbergh, C. 1995. Composition of eared grebe and western grebe eggs. – Condor 97: 1062–1064.

Howe, H. F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the common grackle. – Ecology 57: 1195–1207.

Hussell, D. J. T. 1972. Factors affecting clutch size in Arctic passerines. – Ecol. Monogr. 42: 317–364.

Jager, T. D., Hulscher, J. B. and Kersten, M. 2000. Egg size, egg composition and reproductive success in the oystercatcher *Haematopus ostralegus*. – Ibis 142: 603–613.

Lack, D. 1968. Ecological adaptation for breeding in birds. – Methuen, London.

Lemel, J. 1989. Body-mass dependent fledging order in the great tit. – Auk 106: 490–492.

Lipar, J. L. and Ketterson, E. D. 2000. Maternally derived yolk testosterone enhances the development of the hatching muscle in the red-winged blackbird *Agelaius phoeniceus*. – Proc. R. Soc. B 267: 2005–2010.

Littell, R. C., Milliken, G. A., Stroup, W. W. and Wolfinger, R. D. 1996. SAS system for mixed models. – SAS Institute Inc., Cary, NC.

Magrath, M. J. L., Brouwer, L. and Komdeur, J. 2003. Egg size and laying order in relation to offspring sex in the extreme sexually size dimorphic brown songlark, *Cinclorhamphus cruralis*. – Behav. Ecol. Sociobiol. 54: 240–248.

Meathrel, C. E. and Ryder, J. P. 1987. Intraclutch variation in the size, mass and composition of ring-billed gull eggs. – Condor 89: 364–368.

Michl, G., Török, J., Péczely, P., Garamszegi, L. Zs. and Schwabl, H. 2005. Female collared flycatchers adjust yolk testosterone to male age but not to attractiveness. – Behav. Ecol. 16: 383–388.

Morgan, I. J. and Metcalfe, N. B. 2001. Deferred costs of compensatory growth after autumnal food shortage in juvenile salmon. – Proc. R. Soc. B 268: 295–301.

Nilsson, J.-Å. 1993. Energetic constraints on hatching asynchrony. – Am. Nat. 141: 158–166.

Nilsson, J.-Å. and Gårdmark, A. 2001. Sibling competition affects individual growth strategies in marsh tit, *Parus palustris*, nestlings. – Anim. Behav. 61: 357–365.

Nilsson, J.-Å. and Svensson, M. 1996. Sibling competition affects nestling growth strategies in marsh tits. – J. Anim. Ecol. 65: 825–836.

Oddie, K. 2000. Size matters: competition between male and female great tit offspring. – J. Anim. Ecol. 69: 903–912.

Ojanen, M., Orell, M. and Väisänen, R. A. 1978. Egg and clutch sizes in four passerine species in northern Finland. – Ornis Fenn. 55: 60–68.

Ostreiher, R. 1996. Food division in the Arabian babbler nest: adult choice or nestling competition. – Behav. Ecol. 8: 233–238.

Price, K. and Ydenberg, R. 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. – Behav. Ecol. Sociobiol. 37: 201–208.

Reynolds, S. J., Schoech, S. J. and Bowman, R. 2003. Nutritional quality of prebreeding diet influences breeding performance of the Florida scrub-jay. – Oecologia 134: 308–316.

Ricklefs, R. E. 1965. Brood reduction in the curve-billed thrasher. – Condor 67: 505–510.

Rosivall, B., Török, J. and Szöllősi, E. 2005. Food allocation in collared flycatcher (*Ficedula albicollis*) broods: do rules change with the age of nestlings? – Auk in press.

Royle, N. J., Surai, P. F., McCartney, R. J. and Speake, B. K. 1999. Parental investment and egg yolk composition in gulls. – Funct. Ecol. 13: 298–306.

Sahan, U., Ipek, A. and Yilmaz, B. 2003. The effect of storage temperature and position on embryonic mortality of ostrich (*Struthio camelus*) eggs. – S. Afr. J. Anim. Sci. 33: 38–42.

Schwabl, H. 1993. Yolk is a source of maternal testosterone for developing birds. – Proc. Natl. Acad. Sci. USA 90: 11446–11450.

Schwabl, H. 1996. Maternal testosterone in the avian egg enhances postnatal growth. – Comp. Biochem. Phys. A 114: 271–276.

Schwabl, H., Mock, D. W. and Gieg, J. A. 1997. A hormonal mechanism for parental favouritism. – Nature 386: 231.

Starck, J. M. and Ricklefs, R. E. 1998. Avian growth rate data set. – In: Starck, J. M. and Ricklefs, R. E. (eds). Avian growth and development. Oxford University Press, Oxford, pp. 381–423.

Stenning, M. J. 1996. Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses. – Trends Ecol. Evol. 11: 243–246.

Stjernman, M., Råberg, L. and Nilsson, J.-Å. 2004. Long-term effects of nestling condition on blood parasite resistance in blue tits (*Parus caeruleus*). – In: Stjernman, M. Causes and consequences of blood parasite infections in birds. PhD thesis, Lund University, pp. 85–96.

Török, J. and Tóth, L. 1988. Density dependence in reproduction of the collared flycatcher (*Ficedula albicollis*) at high population levels. – J. Anim. Ecol. 57: 251–258.

Veiga, J. P. 1992. Hatching asynchrony in the house sparrow: a test of the egg-viability hypothesis. – Am. Nat. 139: 669–675.

Viñuela, J. 1997. Adaptation vs. constraint: intraclutch egg-mass variation in birds. – J. Anim. Ecol. 66: 781–792.

Viñuela, J. 2000. Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. – Behav. Ecol. Sociobiol. 48: 333–343.

von Schalkwyk, S. J., Brand, Z., Cloete, S. W. P. and Brown, C. R. 1999. Effects of time of egg collection and pre-incubation treatment on blastoderm development and embryonic mortality in ostrich embryos. – S. Afr. J. Anim. Sci. 29: 154–163.

Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effect on offspring fitness. – Biol. Rev. 68: 35–59.