In the Blackcap Sylvia atricapilla Last-Hatched Nestlings Can Catch up with Older Siblings

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In the Blackcap *Sylvia atricapilla* last-hatched nestlings can catch up with older siblings

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Development during the relatively short time that young spend in the nest is crucial in a bird's life history. The rate of nestling growth strongly depends on numerous environmental and social factors, even within the same species or population. In the present study I examine the relative contributions of brood size, hatching asynchrony, hatching date and feeding rate in determining intraspecific variation in the growth of Eurasian Blackcap *Sylvia atricapilla* nestlings. I found a significant effect of brood size, hatching order and date on nestling development. However, the effect of hatching order and date was significant only for young nestlings and it gradually disappeared with nestling age. The only factor significantly affecting nestling development just before fledging was brood size. Nests of four siblings produced the heaviest young with the longest tarsi. This probably resulted from the highest feeding rate per nestling observed in broods of four nestlings. The study shows that for Blackcaps breeding in a good year a brood size of four is the optimal number, and that younger siblings can catch-up with older nest mates.

Key words: nestling growth, brood size, hatching order, Eurasian Blackcap

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Nestling growth and development during the relatively short time that young spend in a nest can affect their survival (Magrath 1991, Pettifor *et al.* 2001). Despite the evidence of higher survival rates and better recruitment of larger and heavier nestlings (Tinbergen & Boerlijst 1990, Both *et al.* 1999), explanations of these observations are still theoretical. Better developed fledglings may acquire critical motor skills more rapidly than those in poorer condition, which in turn reduces their vulnerability to predators. Larger young may also be more competitive, less prone to post-fledging food shortage and better able to deal with energetic costs during migration. Another consequence of nestling development is the future reproductive success of an individual (Stearns 1992). It has been shown that nestlings in poorer condition are less likely to acquire a mate as adults (Nowicki *et al.* 2000). Thus, irrespective of causation, growth during the nestling period appears to be a crucial stage in a bird's life-history.

Variation in the rate of nestling growth has been demonstrated both between and within species (Remeš & Martin 2002, Zach & Mayoh 1982). Between species, much of the difference in nestling development is explained by predation rate (Bosque & Bosque 1995). As shortening the nesting period is adaptive under heavy nest predation, in these circumstances the rate of nestling development increases. This effect is independent of phylogeny and seems to be the most important factor in differences in growth rate between species (Remeš & Martin 2002). Within species variability in nestling growth may be attributed to the effects of brood size (Bryant 1978), hatching asynchrony (Magrath 1990), date (Verhulst & Nillson 2008, Garcia-Navas & Sanz 2011), parental effort and ability (Naef-Daenzer & Keller 1999), habitat quality (Dawson & Bidwell 2005) and weather (Murphy 1985).

Nestling development therefore strongly depends on numerous environmental and social factors, even within the same species or population. Despite the importance of this, basic information on these factors is still limited or absent for many species. An example is the Eurasian Blackcap *Sylvia atricapilla* – a species widely distributed in the Western Palearctic. Although numerous studies have been conducted on its breeding biology (e.g. Weidinger 2000, 2002, Schaefer 2004, Remeš 2005, Węgrzyn & Leniowski 2011), none of them explored the extrinsic factors affecting nestling development. Therefore, the aim of the current study is to investigate the effects of brood size, hatching asynchrony and date on nestling growth in the Blackcap.

METHODS

Study species

The Blackcap is a small, migratory, open-nesting passerine breeding in Central Europe. It prefers habitat characterized by dense tree and shrub vegetation (Glutz von Blotzheim & Bauer 1991). It builds a thin-walled, open cup nest of 10 cm diameter and 5 cm in height in the shrub and herbaceous layers of forests (Storch 1998). The clutch size is three to five eggs laid on consecutive days. Incubation lasts 12 days and nestlings stay in the nest for another 12 days, but they are able to fledge when 9 days old.

Study area

The study was conducted in 2011, in deciduous forest of the 'Fox hill' Reserve on the outskirts of Rzeszow, south-east Poland. Nests were found by careful inspection of potential sites from mid-April until the end of June, after mapping males' breeding territories in the spring. Nests were checked daily until predated or left by nestlings. Each territory was searched at intervals of up to three days until the nest was found. Only nests with complete clutches were included in the data set. The majority of nests (28 of 35) were found in the laying phase and the remaining found during the incubation phase. The exact hatching date for all nests used in analyses was known. Nests were followed through the nesting period until predated or until nestlings fledged.

Nestling measurements

Measures of nestling mass and tarsus length were taken daily between 18:00 and 20:00 hours. Nestlings were weighed using an electronic scale to the nearest 0.01 g. Tarsus length was measured with callipers to the nearest 0.5 mm. The last measurements in a nest were taken when nestlings were 8 days old (hatching = day 1). Nestlings from three nests were mistnetted and measured on day 11, shortly after leaving the nest. Most cross-sectional analyses were carried out on day 4 (n = 15 nests) and day 8 (n = 12 nests) to explore effects of brood size, hatching asynchrony and hatching date on nestling development both during the phase of intense growth (day 4) and close to fledging (day 8). These ages were chosen primarily for ethical reasons. Longitudinal analyses involved daily measurements of 48 nestlings from 12 nests that successfully fledged.

All nestlings were marked by temporary individually coloured soft plastic rings in the evening of the day they hatched. Temporary plastic rings were replaced by metal ones when nestlings were 5 days old. Marking individuals allowed recognition of first and last nestlings and also longitudinal analyses of changes in their growth.

Additional data

I collected data on feeding rates for 15 nests on day 4 and 12 nests on day 8 (in each analysis I used all available nests with nestlings). Feeding rate was estimated using a diascope at poorly concealed nests, and film from a micro-camera, placed at a distance of about 30 cm from a nest, in the case of well concealed nests. A camera, that was thumb nail size, was additionally masked by a leaf and mounted at least a few hours before filming, so that any effect of placing the camera on parental behaviour was assumed to be absent during filming. In analyses of the effect of brood size on nestling growth I used feeding rate per nestling, calculated as the number of parental visits with food per hour divided by the number of siblings in a nest.

In analyses of the effect of hatching date on nestling growth I divided nestlings into two categories: (1) hatched in May, and (2) hatched in June. I did not use the exact dates of hatching (although they were known) as I assumed that a few days difference among broods is less important than the information on which stage of the breeding season nestlings hatched. This approach allowed comparison of early and late broods.

The weather during the whole breeding season in 2011 was exceptionally stable, with a temperature of 22– 24°C on most days and only a few rainy days. I did not observe brood reduction in any of the nests; however, some nests were abandoned during the egg phase after a day of rain. I did not expect that weather would have had an effect on nestling development (due to its stability across the season), thus I did not include this factor in the analyses.

Statistics

All analyses were conducted using SPSS 16 software (SPSS Inc., Chicago). For the longitudinal analysis of the effect of brood size on nestling growth I used Repeated Measures GLM with daily measurements of mass and tarsus length as within-subject variables and brood size as a between-subject factor. This analysis was carried out for 12 nests (four nests of three nestlings, four nests of four nestlings and four nests of five nestlings) from day 2 to day 8.

In cross-sectional analyses I used Multivariate GLM with brood size as a factor and mass and tarsus length as dependent variables. Cross-sectional analyses were carried out on day 4 (15 nests) and 8 (12 nests) since first hatchlings appeared in a nest.

The effect of the number of siblings on feeding rate per nestling was tested in 15 nests on day 4 and 12 nests on day 8 using ANOVA. Differences in feeding rate between nests of different brood sizes were tested using the Kolmogorov–Smirnof Z-test.

Differences in mass and tarsus length between first- and last-hatched nestlings were tested using a Student's *t*-test. The same method was used in analyses of hatching date (May versus June) on nestling growth.

RESULTS

Clutch and brood sizes

I found 35 nests with complete clutches, of which 2 (5.6%) contained 3 eggs, 9 (25%) contained 4 eggs, 24 (66.7%) contained 5 eggs and 1 nest (2.8%) contained 6 eggs. Nineteen of these nests (52.8%) survived until hatching: brood size varied from 2 to 5 nestlings. Of 19 nests with hatchlings 1 nest (5.26%) contained 2 nestlings, 4 nests (21%) contained 3 nestlings, 8 nests (42.1%) contained 4 nestlings and 6 nests (31.6%) contained 5 nestlings. The modal nest contained 4 siblings. In 8 of 19 nests (42.1%) that survived until the nestling stage I observed partial hatching failure. In 5 nests 1 egg did not hatch and in 3 nests 2 eggs did not hatch. Nestlings successfully fledged from 12 out of 35 nests.

Brood size and nestling growth

LONGITUDINAL APPROACH

Longitudinal analysis to establish the effect of the number of siblings on nestling mass and tarsus length was carried for 12 nests (four nests of three, four and five siblings) between day 2 and 8 of the nesting period. The results of repeated measures GLM revealed a significant effect of the number of nest-mates on both nestling mass ($F_2 = 23.97$, $P < 0.001$) and tarsus length ($F_2 = 12.9$, $P < 0.001$).

CROSS-SECTIONAL APPROACH

To study the pattern of the differences in nestling growth in relation to the number of siblings I conducted cross-sectional analyses on day 4 (the mid-point of the nesting period) and on day 8 (the last day of nesting period before nestlings are able to leave the nest). Biometry of broods of three, four and five siblings on day 4 and 8 is given in Table 1.

The number of siblings significantly affected nestling mass (GLM: $F_2 = 40.86$, $P < 0.001$, $n = 61$) and tarsus length (GLM: $F_2 = 4.01$, $P = 0.025$, $n = 61$) on day 4. Nestlings from nests containing three siblings were significantly lighter and had shorter tarsi than nestlings from nests of four ($t_{34} = –4.31$, $P < 0.001$ and $t_{34} = –3.03$, $P = 0.004$, respectively) and five siblings ($t_{35} = –5.31$, $P < 0.001$ and $t_{35} = –3.32$, $P = 0.003$, respectively). There was no significant difference in mass ($t_{47} = –1.3$, $P = 0.2$) and tarsus length ($t_{47} = –0.26$, $P = 0.98$) between nestlings from nests of four and five siblings (Figure 1).

On day 8 the number of siblings also significantly affected nestling mass (GLM: $F_2 = 8.63$, $P = 0.001$,

Table 1. Nestling mass and tarsus length, and feeding rate in relation to brood size at 4 and 8 days of age for nestling Blackcaps.

Parameter	**Age** (days)		**Brood size**		
			3	**4**	**5**
Mass (g)	4	Mean ± SD	6.05 ± 0.78	7.24 ± 0.82	7.55 ± 0.64
		n	12	24	25
	8	Mean ± SD	13.04 ± 0.40	13.62 ± 0.68	13.01 ± 0.75
		n	12	16	20
Tarsus (cm)	4	Mean ± SD	1.35 ± 0.07	1.49 ± 0.14	1.49 ± 0.12
		n	12	24	25
	8	Mean ± SD	2.14 ± 0.1	2.23 ± 0.06	2.18 ± 0.13
		n	12	16	20
Feeding rate (*n*/hour/nestling)	4	Mean ± SD	1.99 ± 0.25	2.88 ± 0.48	2.3 ± 0.26
		n	12	24	25
	8	Mean ± SD	4.17 ± 0.84	5.38 ± 0.25	4.7 ± 0.38
		n	12	16	20

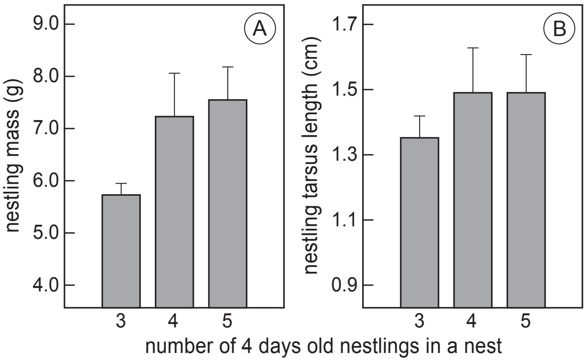

Figure 1. Mean mass (A) and tarsus length (B) by brood size; nestlings four days old. Error bars show ± 1 SD.

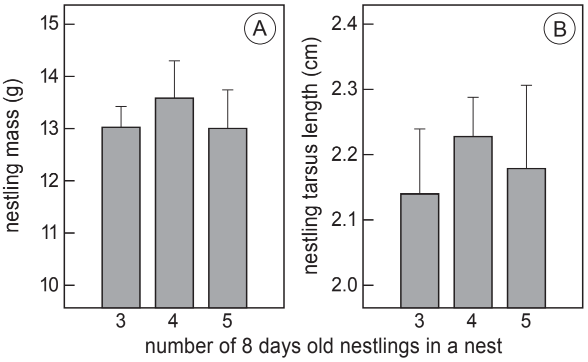

Figure 2. Mean mass (A) and tarsus length (B) by brood size; nestlings eight days old. Error bars show ± 1 SD.

$n = 48$) and tarsus length (GLM: $F_2 = 4.52$, $P = 0.025$, $n = 61$). However, the pattern of differences in nestling body growth in nests of three, four and five siblings on day 8 was different than that observed on day 4 (Figure 2). Similarly to day 4, nestlings from nests containing four siblings were significantly heavier ($t_{26} = -2.25$, $P = 0.032$) and had longer tarsi ($t_{26} = 0.1$, $P = 0.92$) than nestlings from nests of three siblings but on day 8 they were also significantly better developed than nestlings from the nests of five chicks (mass: $t_{34} = 2.35$, $P = 0.023$, tarsus length: $t_{34} = 1.55$, $P = 0.13$). There were no significant differences between mass ($t_{30} = 0.1$, $P = 0.92$) and tarsus length ($t_{30} = -0.83$, $P = 0.42$) of nestlings from nests of three and five siblings.

Feeding rate per nestling in relation to brood size

The number of siblings in a nest significantly affected feeding rate per nestling on day 4 and 8 ($F_2 = 6.862$, $P = 0.015$, $n = 61$ and $F_2 = 4.84$, $P = 0.037$, $n = 48$, respectively). In both cases feeding rate was the highest for nestlings from the nest of four siblings (Figure 3). The difference in feeding rate between nestlings from nests of four and five siblings was not statistically significant on day 4 ($Z = -1.742$, $P = 0.08$), however it became significant on day 8 ($Z = -2.084$, $P = 0.037$). Nestlings from nests of four siblings were fed significantly more often than nestlings from nests of three siblings irrespective of the stage of nesting period ($Z = -2.045$, $P = 0.041$ on day 4 and $Z = -2.084$, $P = 0.037$ on day 8). There were no significant differences in feeding rate per nestling between nests containing three and five siblings, both on day 4 and 8 ($Z = -1.479$, $P = 0.139$ and $Z = -1.169$, $P = 0.243$, respectively).

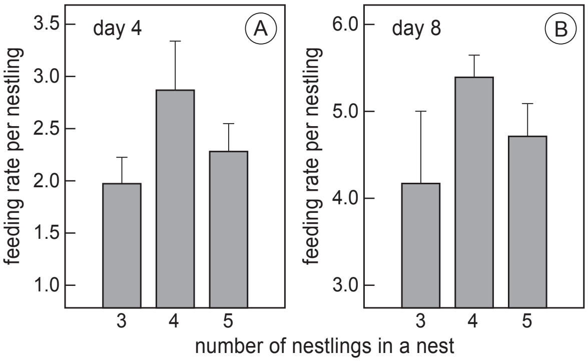

Figure 3. Feeding rate (number of visits per hour per nestling) by brood size; (A) four day old nestlings, and (B) eight day old nestlings. Error bars show ± 1 SD.

Asynchronous hatching and nestling growth

First, I compared mass and tarsus length of two nestlings categories (first vs. last-hatched) from eight nests of asynchronous hatching in the consecutive days between day 2 and 8 since first hatchlings in the nest (the first-hatched nestlings were 1 day older than the last). Last-hatched nestlings were significantly lighter than the first-hatched ($t_6 = 12.58$, $P < 0.001$, Figure 4A) and had shorter tarsi ($t_6 = 12.15$, $P < 0.001$, Figure 4B).

Secondly, I compared mass and tarsus of first and last-hatched nestlings according to their real age (i.e. first-hatched nestlings in their second day of life were compared to last-hatched nestlings in their second day of life, and so on). In this approach last-hatched nestlings appeared significantly heavier ($t_5 = -3.139$, $P = 0.026$, Figure 5A) and had longer tarsi ($t_5 = -2.727$, $P = 0.041$, Figure 5B).

The difference in body mass and tarsus length between first and last nestlings was most pronounced in the first days after hatching and it gradually disappeared in consecutive days (Figure 6). One day old last-hatched nestlings were 32% lighter than their two day old siblings and had 16% shorter tarsi, but on day

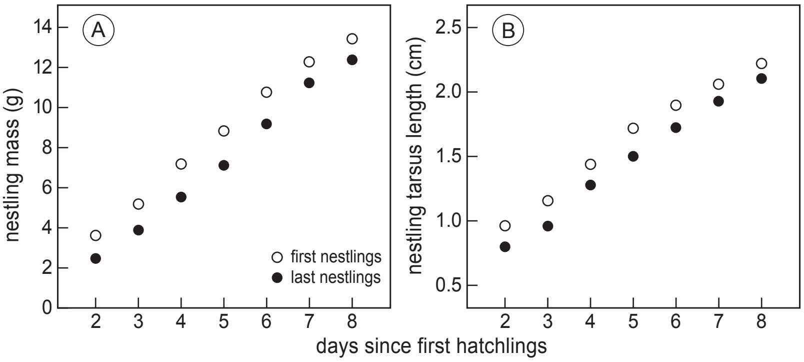

Figure 4. Body mass (A) and tarsus length (B) for first and last-hatched nestlings on consecutive days since the first nestlings hatched.

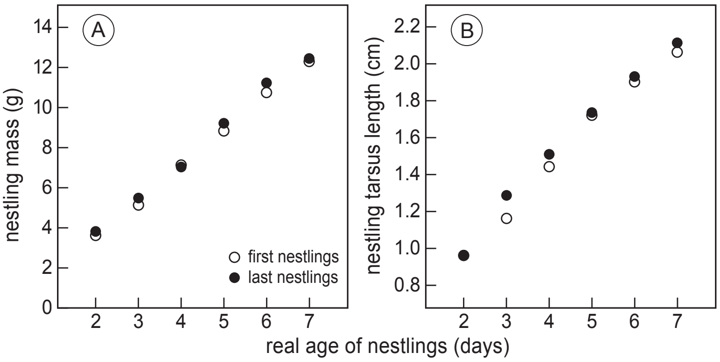

Figure 5. Body mass (A) and tarsus length (B) for first and last-hatched nestlings in relation to their real age.

7 were only 8% lighter and had 5% shorter tarsi than their older nest-mates. This shows that last-hatched nestlings were able to decrease the initial difference between themselves and first-hatched nestlings by growing faster.

Nestlings from three broods were mistnetted just after fledging (day 11). Body mass and tarsus length were not significantly different between first- and last-hatched siblings (t_2 = 0.12, P = 0.92), which demonstrates that the last nestlings to hatch had been able to fully catch up with the development of their siblings at the time of leaving the nest.

Hatching date and nestling growth

On day 4 nestlings that hatched in May were significantly heavier (t_{59} = 3.08, P = 0.003) and had longer tarsi (Table 2) than hatchlings from June. This difference however, disappeared on day 8 and nestlings that hatched in May and June had similar mass and tarsus length at the end of nesting period (Table 2).

To investigate the difference between nestlings from May and June I analyzed their mass and tarsus length just after hatching. 1-day-old hatchlings from May were both heavier and had longer tarsi than hatchlings from June at the same age (Table 2) and the differences were highly significant (t_{72} = 3.5, P = 0.001 and t_{72} = 3.09, P = 0.003, respectively). This suggests that the differences do not arise after hatching, but result from smaller and/or lighter eggs laid in breeding attempts in June.

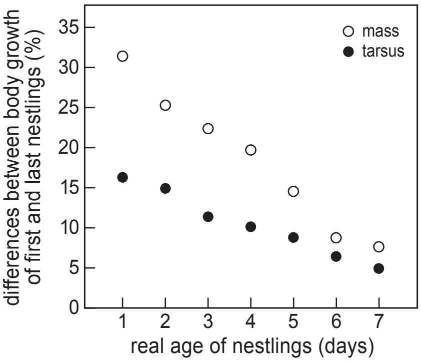

Figure 6. Percentage difference in mass and tarsus length between last-hatched nestlings and their older siblings on consecutive days.

DISCUSSION

My study demonstrated that brood size significantly affected nestling growth and feeding rate per nestling in Blackcaps. I also found a significant effect of hatching order and date on nestling development.

Brood size and nestling growth

Broods of four siblings produced the best developed nestlings both in terms of mass and tarsus length. This resulted from the fact that nestlings from broods of four were fed more frequently than nestlings from broods of three or five, and this was especially pronounced at the end of nesting period. Parents of broods of five sibs were not able to feed their young sufficiently in the period of the highest food demand (later in the nestling period), which has also been reported in other studies (de Kogel & Prijs 1996). Broods of three siblings showed significantly lower development than larger broods. This is in contrast to studies that demonstrated a negative relationship between brood size and nestling growth (Cronmiller & Thompson 1980, Naguib *et al.* 2004, but see Krebs 1999). One possible explanation of poorer development in nestlings from broods of three may be lower quality parents. Broods of three siblings resulted from hatching failure in May (two nests) and small clutch size in June (two nests). Both factors suggest lower quality parents. This assumption is supported by the fact that feeding rate per nestling in broods of three on day 4 was significantly lower than in larger broods of four and five sibs.

Asynchronous hatching and nestling growth

During the whole nesting period last-hatched nestlings were significantly lighter and smaller than their older siblings, which is typical for asynchronous hatching. However, the difference in development decreased with nestling age, due to a higher growth rate in last-hatched nestlings, despite the disadvantages of the size hierarchy. This is in contrast to other studies that demonstrated enhanced growth of first-hatched nestlings that simultaneously enjoyed priority in access to food (Forbes *et al.* 1997). The pattern of growth of the last nestlings observed in my study may be explained by selective feeding of smaller nestlings (Gottlander 1987) and/or the last-hatched nestlings may be more competitive, for example due to higher concentrations of yolk androgens (Schwabl 1996, Eising *et al.* 2001) or larger final eggs. This assumption may be supported by the fact that last-hatched nestlings were significantly more developed than their older siblings when compared at the same age. It suggests that they hatched from larger eggs (Forbes & Wiebe 2010). If so, asynchronous hatching in Blackcaps may be a by-product of the onset of incubation before clutch completion, in which females compensate for the shortening of incubation of the last eggs by increasing their quality and/or volume. Such a strategy would be adaptive at high nest predation levels, as observed in Blackcaps (Remeš 2005, Węgrzyn & Leniowski 2011), because an increase in the probability of brood survival (through shortening of the nestling period) would not be achieved at the cost of the quality of the last hatchlings. Thus, the results of my study suggest that asynchronous hatching in Blackcaps is best explained by the *nest failure hypothesis* (Clark & Wilson 1981), which argues that an earlier start of incubation reduces the risk of predation. My findings are also consistent with the *quality-assurance hypothesis* (Amundsen & Slagsvold 1998), which states that hatching asynchrony insures the quality of at least some of the nestlings. The comparison of development of the first- and last-hatched nestlings from three nests that were mistnetted shortly after fledging (in day 11th) did not show any significant differences in mass or tarsus length. It demonstrates that, at least in these broods, the last nestlings were able to fully catch up with their older

Table 2. Nestling mass and tarsus length at 1, 4 and 8 days of age in relation to hatching date (May versus June).

Age (days)	**1**		**4**		**8**	
	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*
Mass (g)						
May	2.23± 0.22	42	7.29± 0.89	29	13.21± 0.78	24
June	1.98± 0.29	32	6.45± 1.05	28	13.21± 0.91	24
Difference	$t_{72} = 3.5$ $P = 0.001$		$t_{59} = 3.08$ $P = 0.003$		$t_{46} = –0.13$ $P = 0.99$	
Tarsus length(mm)						
May	0.82± 0.06	42	1.44± 0.12	29	2.17± 0.11	24
June	0.77± 0.07	32	1.26± 0.09	28	2.18± 0.09	24
Difference	$t_{72} = 3.09$ $P = 0.003$		$t_{59} = 4.11$ $P < 0.001$		$t_{46} = –0.61$ $P = 0.55$	

siblings at the time of leaving the nest. Additionally, I did not observe a single case of brood reduction in any of the studied nests. However, this cannot be taken as evidence against the *brood reduction hypothesis* (Lack 1954), which states that hatching asynchrony is adaptive in unpredictable environments, because the weather was extremely good during the whole season. Therefore, depending on circumstances, both hypotheses may be true in Blackcaps: last hatchlings may be designed for more effective growth in favourable conditions, but being younger, and thus relatively smaller, they are still the first to die during periods of food shortage. It would be useful for future studies to confirm whether the last-hatched nestlings in Blackcap asynchronous broods hatch from larger/androgen richer eggs. This would further support both the *nest failure* and the *quality-assurance hypotheses*.

Hatching date and nestling growth

Nestlings that hatched in May were heavier and had longer tarsi than those hatched in June, however this difference disappeared before fledging. This shows that irrespective of initial differences, late broods were able to reach mass and size similar to early broods. This is in contrast to other studies which have demonstrated that nestlings from earlier broods developed better (e.g. Järvinen & Ylimaunu 1984, Verhulst & Nilsson 2008).

Although I did not ring adult individuals in the studied population, I assumed that the majority of the nestlings hatched in June came from re-nesting attempts by pairs whose nests were previously predated. This assumption was made in case of the nests that were built shortly after predation within the same territories. However, I also recorded some new breeding pairs on new territories. In these cases it was impossible to say whether the adults were late arrivals or whether they came from outside of my study area and established new territories after previous nest failure. Irrespective of the scenario, the initial differences in development between early and late broods were noticeable on the day of hatching, so they probably resulted from smaller eggs laid later in the season. Egg volume may be smaller due to reserves depletion in relaying females (Hegyi 1996). As egg size reflects the lipid and protein content of the eggs (e.g. Williams 1994, Jager *et al.* 2000), larger eggs result in larger hatchlings that grow faster and have higher survival probabilities (Whittingham *et al.* 2007, Forbes & Wiebe 2010). Alternatively, under the *parental-quality hypothesis*, late breeders often recruit from young and inexperienced individuals (Forslund & Pärt 1995), that lay smaller eggs (Christians 2002), arrive later on breeding grounds (Nol & Smith 1987) and/or breed on territories of poorer quality (Alatalo *et al.* 1986). Whether Blackcap eggs hatching in June were smaller due to resource depletion in re-laying females or lower quality of late breeders needs further investigation. The most interesting point is that the initial differences in growth between early and late broods had no long-lasting effect on nestling development. This might have resulted from the good environmental conditions during the study period. On the other hand, the Blackcap suffers from high nest predation (Weidinger 2000, 2002, Remeš 2005, Węgrzyn & Leniowski 2011). First broods rarely succeed and re-nesting attempts are common. Thus, one might expect a strategy that ensures high quality nestlings throughout the breeding season. For example, smaller egg volumes resulting from re-nesting may be compensated for by higher concentrations of yolk androgens, which in turn accelerate nestling growth (Eising *et al.* 2001). Alternatively, parents may invest more in feeding late broods, which can positively affect nestling development. Both assumptions seem worth testing in future studies of Blackcap breeding ecology.

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SAMENVATTING

De groeisnelheid van nestjongen hangt van talloze factoren af. Bij dit Poolse onderzoek aan Zwartkoppen *Sylvia atricapilla* werd gekeken naar de invloed van de broedselgrootte, de volgorde van het uitkomen binnen het nest, de uitkomstdatum en het aantal keren dat er per dag werd gevoed op de groeisnelheid van de jongen. De groeisnelheid bleek vooral af te hangen van de broedselgrootte. Tijdens de eerste dagen na uitkomen waren de relatieve leeftijd binnen het nest en de datum van uitkomen ook van belang, maar deze effecten verdwenen naarmate de jongen ouder werden. Jongen in broedsels van vier kregen het meeste voedsel. Ze werden ook het zwaarst en kregen de langste tarsi. Er wordt daarom geconcludeerd dat in jaren met voldoende voedsel de optimale broedselgrootte vier bedraagt. (YIV)

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