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Source: Acta Ornithologica, 39(2) : 176-179

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/068.039.0204

ACTA ORNITHOLOGICA
Vol. 39 (2004) No. 2

Relationship between laying order and egg dimensions in the Blackcap *Sylvia atricapilla*

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Dolenec Z. 2004. Relationship between laying order and egg dimensions in the Blackcap *Sylvia atricapilla*. Acta Ornithol. 39: 176–179.

Abstract. This study analyzes the influence of egg laying order on egg dimensions (especially on egg volume) and on the size of the last egg laid in a Blackcap clutch. The research was carried out in deciduous woodland in NW Croatia during 2002 and 2004. The analyses covered only clutches with five eggs (the dominant size of the first clutch in the study area), where the first eggs were laid on the same day (5 May 2002 and 11 May 2004). The present study suggests that the Blackcap may employ a strategy of increasing the egg volume of each successive egg laid, which may reduce size hierarchy between nestlings and prevent competition between them.

Key words: Blackcap, *Sylvia atricapilla*, egg dimensions, egg volume, laying order

Received — June 2004, accepted — Sept. 2004

INTRODUCTION

The question of how an organism allocates resources to diverse traits is becoming a central issue in life history analyses (Cichoń 1997). Attention has recently been focused on egg size variation (weight, or index volume derived from the length and breadth of eggs) as one of several mechanisms that regulate brood size (e.g. Haftorn 1986). Nestling hatched from larger eggs grow faster, achieve higher fledgling mass, or have higher survival rates (e.g. Schifferli 1973, Hegyi 1996, Amat et al. 2001). Many bird species show significant egg size variation with laying sequence and hatch their clutches asynchronously (Hebb 1994). For example, egg size decreases with the laying order in some bird species (e.g. Bancroft 1984, Rofstadt & Sandvik 1985), but it increases in other (e.g. Murphy 1994, Enemar & Arheimer 1999), whereas in some species the laying order has no influence at all on egg size (e.g. Bańbura & Zieliński 1995, Dolenec 2002). Hatching asynchrony is a result of starting of incubation before egg laying is complete. Hatching asynchrony producing a competitive difference between early- and late-hatched young so that the latter may be sacrificed if food is insufficient to feed adequately the whole brood (e.g. O'Connor 1978, Magrath 1990). Trends for eggs to become larger or smaller during the order of laying, would mitigate or accelerate the disadvantages suffered by late-hatched young. Slagsvold et al. (1984) analyzed intra-clutch variation in egg size in 67 bird species and identified two strategies: birds which lay relatively larger final eggs are adopting the "brood survival strategy" (the last nesting is capable of rivalry with its older siblings), whereas birds which lay relatively small final eggs are adjusting to the "brood reduction strategy" (the last nestling will be sacrificed in the event of food shortage).

This study has two tasks. First, to investigate the influence of laying order on egg dimensions. Second, to calculate the deviation of the final egg from mean referred here as % D (according to Slagsvold et al. 1984).

STUDY AREA AND METHODS

The study was conducted in Hrvatsko Zagorje region in NW Croatia (45°58′–46°10′N, 15°50′–6°08′E), in 2002 and 2004. The study area is a mixed farming area with small meadows and arable land. The arable land contains small woods (up to 10 ha) dominated by Common Oaks *Quercus robur* and Hornbeams *Carpinus betulus*. As laying time approached, nests were checked daily to determine the date of the first egg laid. Eggs were marked with pen. All eggs were measured to the nearest 0.01 mm (maximum length and breadth). Nests with abandoned clutches were excluded from analysis. A clutch size was assigned when the same number of egg was recorded on two consecutive visits to the nest. As different internal and external factors can obscure a potential pattern of variation in egg size in relation to the laying sequence (Bańbura & Zieliński 1995), this analysis includes only first clutches with 5 eggs (n = 22, the modal clutch size, Dolenec 1994), where first eggs were laid on the same day (5 May 2002 and 11 May 2004). Egg volume (V) was calculated from the equation by Hoyt (1979):

$$V = 0.51 \times L \times B^2$$

where: L is maximum egg length, B is maximum egg breadth. Egg shape index (ES) was calculated using the Schönwetter (1967–1976) formula:

$$ES = L/B$$

The deviation of the final egg from mean was referred here as % D. This value, was calculated according to Slagsvold et al. (1984):

$$\%D = \frac{(VF - VM)100\%}{VM}$$

in which VF = volume of the final egg and VM = mean egg volume of the clutch.

General statistical procedures followed the standard methods (Sokal & Rohlf 1981), p–values higher than 0.05 were considered non-significant.

RESULTS AND DISCUSSION

There were no statistically significant differences for egg dimensions in 2002 an 2004 (Table 1). In 2002, there was a significant increase of egg breadth (correlation coefficients: r = 0.408, p = 0.003, number of clutches = 10, number of eggs = 50) and egg volume (r = 0.383, p = 0.006) in relation to the laying order. The correlation of egg length (r = 0.141, p = 0.33) and egg shape index (r = 0.112, p = 0.44) in relation to the laying order

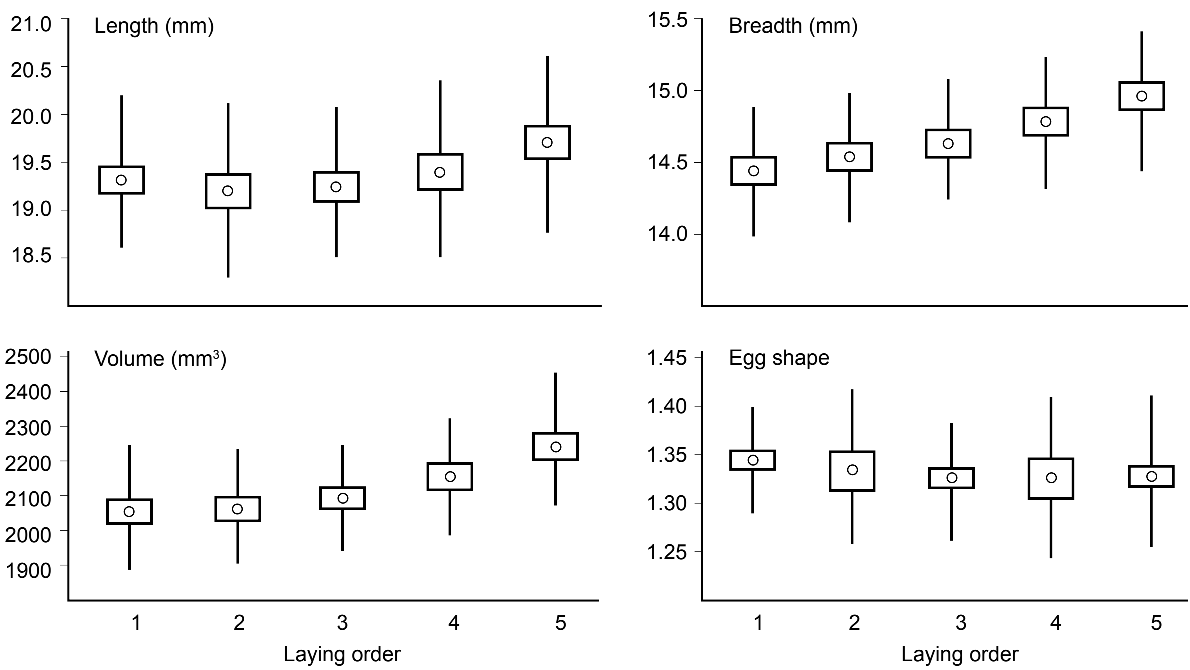

Fig. 1. Variation in egg dimensions in relation to the laying order. Circles indicate the mean, vertical lines one standard deviation on either side of the mean and boxes one standard error on either side of the mean. Only first clutches included.

Table 1. Egg dimensions in five-egg clutches (50 eggs in 2002 and 60 eggs in 2004). SD — standard deviation, ns — non-significant (p > 0.05).

Variable	Year	Mean ± SD	Range	ANOVA
Length (mm)	2002	19.21 ± 0.81	17.64–20.71	$F_{1,108}$ = 3.029, ns
	2004	19.55 ± 0.79	17.91–21.04	
	Total	19.39 ± 0.80	17.64–21.04	
Breadth (mm)	2002	14.71 ± 0.43	13.73–15.62	$F_{1,108}$ = 2.107, ns
	2004	14.61 ± 0.46	13.50–15.79	
	Total	14.66 ± 0.45	13.50–15.79	
Volume (mm^3)	2002	2119.93 ± 160.01	1807.01–2460.03	$F_{1,108}$ = 0.081, ns
	2004	2128.22 ± 176.19	1784.59–2511.81	
	Total	2124.41 ± 168.26	1784.59–2511.81	
Shape index	2002	1.31 ± 0.07	1.16–1.47	$F_{1,108}$ = 3.581, ns
	2004	1.34 ± 0.08	1.15–1.49	
	Total	1.33 ± 0.07	1.15–1.49	

was not statistically significant. In 2004, there was a significant increase of egg breadth (r = 0.329, p = 0.010, number of clutches = 12, number of eggs = 60) and egg volume (r = 0.328, p = 0.011) in relation to the laying order. The correlation of egg length (r = 0.154, p = 0.24) and egg shape index (r = 0.122, p = 0.36) in relation to the laying order was not statistically significant (Table 2). For clutches of 5 eggs values of %D in 2002 and 2004 was 5.28 and 5.04, respectively (Fig. 1).

During the last few decades egg sizes (egg weight and/or egg volume) have been used in investigations of problems related to breeding biology. Regional trends in clutch size were discovered long ago, but the corresponding knowledge regarding egg dimensions is still scanty (Enemar & Arheimer 1999). In several species, the egg size has been found to be positively correlated with the weight of the hatchling (e.g. Schifferli 1973). Slagsvold et al. (1984) found out that the relative size of the last egg was significantly larger in open-nesting than hole-nesting passerines. According to their study, the mean %D-value was 3.56 for 17 bird species. Slagsvold´s et al. (1984) study for the Blackcap gives data for only one 4-egg nest, %D = 7.93. To my knowledge, no other egg volume data of importance have been published for this species. The present study suggests that the Blackcap possibly employs a strategy of increasing egg volume in laying order, which may reduce size hierarchy between nestling and may prevent competition between them (significant increase in egg volume with the progressive laying order and high positive %D-value). A large final egg will increase the probability that the nesting hatched from such an egg will fledge successfully. This is consistent with the view put forward by Howe (1976), that larger egg size represent parental effort to increase the survival chances of the late hatched young.

Table 2. Correlation coefficients for various egg dimensions in relation to the laying order of 5-egg clutches — 10 in 2002 and 12 in 2004 with number of eggs measured 50 and 60, respectively. * — p < 0.05, ** — p < 0.01.

Year	Variable			
	Length	Breadth	Volume	Shape index
2002	0.141	0.408**	0.383**	0.112
2004	0.154	0.329*	0.327*	0.109
Total	0.145	0.360**	0.351**	-0.096

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STRESZCZENIE

[Zależność między kolejnością składania jaj a ich wielkością u pokrzewki czarnołbistej]

Badania prowadzono w lasach liściastych północno-zachodniej Chorwacji w 2002 i 2004 r. Analizie poddano wyłącznie lęgi składające się z 5 jaj (najczęstsza wielkość zniesienia tego gatunki na badanych terenach), w których pierwsze jaja pojawiły się tego samego dnia.

Stwierdzono, że wielkość jaj różniła się pomiędzy sezonami badań (Tab. 1). Kolejność składania jaj istotnie wpływała na ich szerokość i objętość, zaś nie stwierdzono takiego związku z długością i kształtem (określanym stosunkiem długości do szerokości) (Tab. 2, Fig. 1). Uzyskane wyniki wskazują, że pokrzewki czarnołbiste składają coraz to większe jaja, co może redukować różnice w wielkości piskląt, a przez to zapobiegać konkurencji między nimi.