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Egg size variation in the Collared Flycatcher *Ficedula albicollis* in the Białowieża Forest (NE Poland)

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Abstract. 445 eggs of the Collared Flycatcher from 82 clutches were measured during three breeding seasons (1997–1999). The mean length was 17.82 ± 0.80 mm, breadth — 3.45 ± 0.37 mm and volume — 1.65 ± 0.14 cm³. Egg dimensions were positively correlated. No significant differences in egg sizes during the three seasons were found. This suggests that the environmental conditions in the Białowieża Forest during the study period did not change or had no influence on egg size. Laying sequence had no influence on egg dimensions; only egg length depended on clutch size. Some characteristics of the females did affect the size of eggs: heavier birds and those with longer tarsi laid larger eggs. Older females did not lay significantly larger eggs than younger females. In conclusion, egg size in the Collared Flycatcher from the Białowieża Forest appears to be influenced more by the characteristics of the female than by environmental conditions.

Key words: Collared Flycatcher, *Ficedula albicollis*, egg size, laying date, laying order, clutch size

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INTRODUCTION

Production of large eggs is very exhausting as it absorbs 40% or more of the daily production of energy (Ricklefs 1974, Walsberg 1983). Larger species lay bigger eggs in smaller clutches. Precocial birds have generally larger eggs than altricial ones. In many species size of eggs significantly influences the size of nestling (Järvinen & Ylimaunu 1984, Williams 1994). Bigger eggs contain more nutrients (Williams 1994) thus nestling hatching from larger eggs are larger, grow faster and survive better than those from smaller eggs (Perrins 1996).

Two groups of factors may influence the size of eggs: environmental conditions and characteristics of female. In the first group of factors is food abundance and, indirectly, ambient temperature (Ojanen et al. 1981). Both these factors may influence female condition. Variation of egg size may also be affected by heritable features (Ojanen et al. 1979, Potti 1993).

In this work we also studied the effect of laying sequence on variation of egg size. This phenomenon has been explained in adaptive or non-adaptive terms. Houe (1976) determined laying sequence as an adaptive value, however Slagsvold & Lifjeld (1989) demonstrated some evidence of a proximate constraint.

Hitherto only Cichoń (1997) analysed the influence of some factors on variation of egg weight in the Collared Flycatcher. This small migratory bird builds nests in natural tree cavities or in nest-boxes if available. In the Białowieża Forest females begin to lay eggs around 10 May. A clutch contains 4 to 8 eggs, which hatch after two weeks and young usually fledge after further two weeks. The Collared Flycatcher breeds only once in a season, but sometimes after a loss of brood it starts a replacement clutch.

The aim of this work was to examine the influence of some factors, such as female characteristics (age, wing length, tarsus length and weight),

clutch size and laying sequence on variation of Collared Flycatcher's egg size.

STUDY AREA AND METHODS

The material was collected in the Białowieża Forest (52°41'N, 23°52'E) in 1997–1999. The study plot was situated in oak-hornbeam *Tilio-Carpinetum* stands, similar to the plot „Entrance” described by Tomiałojć et al. (1984). We used 60 nestboxes hung 25 m apart each to other in 4 rows each distanced from each by 50 m. Eggs were measured (length and breadth) using sliding callipers to the nearest 0.1 mm. To calculate egg volume the formula: $V = 0.51 \times \text{length} \times \text{breadth}^2$ was used, following Potti (1993). To determine laying sequence each new egg appearing in a nest was individually marked. Laying sequence was studied during two breeding seasons (1997–1998). Clutches were divided into early and late ones according to median date of laying first egg. In 1997 the median date was 16 May, 11 May in 1998 and 19 May in 1999. Replacement clutches were excluded from the analysis.

Females were captured during incubation or in the feeding period. The following measurements were taken from captured birds: body mass (with the use of Pesola spring balance), wing length (maximum chord, Kelm 1970) and tarsus length. The age (one-year old or older) of captured birds was determined on the basis of plumage (Svensson 1992).

To calculate correlations between dimensions of eggs and to analyse the influence of some factors like the laying term, clutch size and female characteristics, mean parameters of eggs from each clutch were used.

RESULTS

Measurements of 117 eggs from 22 clutches were taken in 1997, 165 eggs from 33 clutches in 1998 and 163 from 27 clutches in 1999 (Table 1). The correlation between length and breadth was highly significant (Fig. 1). None of egg dimensions (length, breadth and volume, respectively) differed significantly between years (ANOVA; $F_{2,73} = 0.13$, ns; $F_{2,73} = 1.26$, ns; $F_{2,73} = 0.87$, ns), but the largest eggs were laid in 1999 (Table 2). Slightly bigger eggs were found in earlier clutches (Table 3), as compared with late clutches. However, only the length and the volume differed significantly

Table 1. Variation of egg (n = 445) dimensions (pooled data).

	Mean ± SD	Min–Max
Length (mm)	17.82 ± 0.80	15.8–19.8
Breadth (mm)	13.45 ± 0.37	12.3–14.5
Volume (cm ³)	1.65 ± 0.14	1.23–2.04

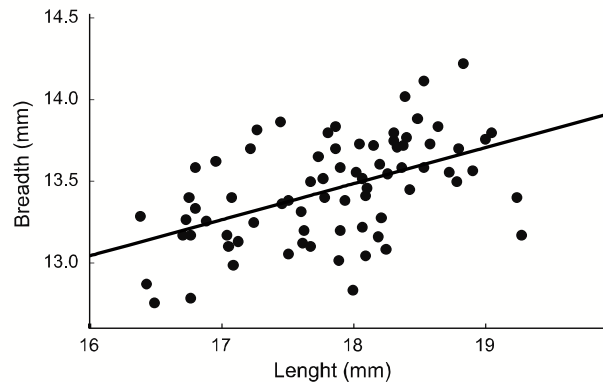


Fig. 1. The correlation between length and breadth of eggs ($r = 0.50$, $p < 0.01$, $n = 75$ clutches).

Tab. 2. Annual variation in the egg dimensions. N — number of clutches.

	N	Mean ± SD	Min–Max
Length (mm)			
1997	22	17.77 ± 0.93	14.35–19.05
1998	33	17.80 ± 0.84	16.40–19.30
1999	27	17.81 ± 0.72	16.42–18.90
Breadth (mm)			
1997	22	13.39 ± 0.61	11.00–14.11
1998	33	13.34 ± 0.30	12.80–14.02
1999	27	13.51 ± 0.32	12.88–14.23
Volume (cm ³)			
1997	22	1.65 ± 0.14	1.27–1.88
1998	33	1.62 ± 0.13	1.37–1.84
1999	27	1.66 ± 0.12	1.39–1.94

Table 3. Egg size in early (n = 48) and late (n = 28) clutches.

	Mean	Min–Max
Length (mm)		
early	17.96 ± 0.74	15.9–19.8
late	17.63 ± 0.84	15.8–19.7
Breadth (mm)		
early	13.46 ± 0.34	12.3–14.5
late	13.42 ± 0.40	12.4–14.1
Volume (mm ³)		
early	1.66 ± 0.13	1.29–2.04
late	1.62 ± 0.15	1.39–1.98

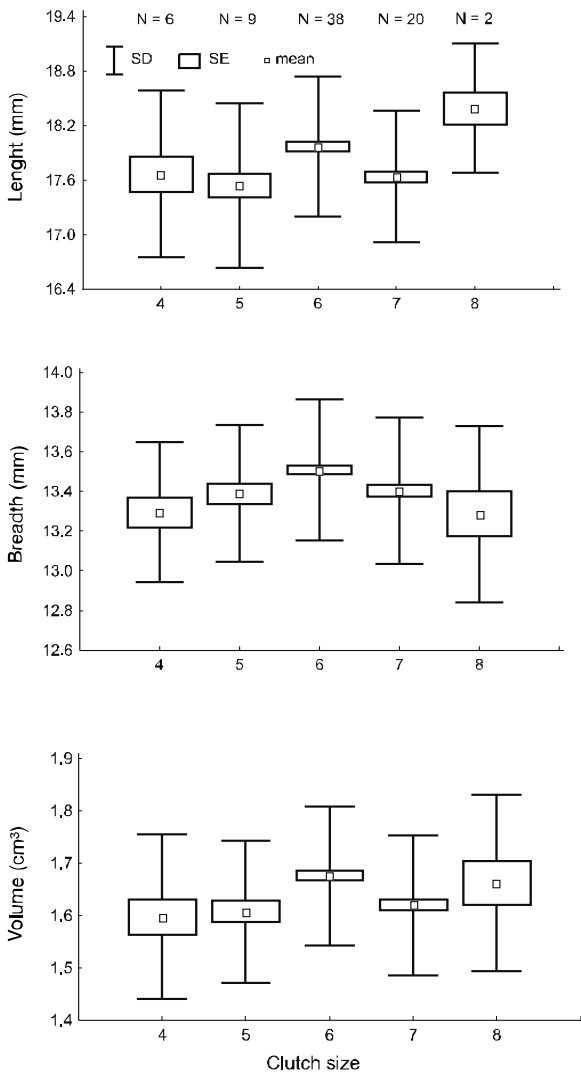


Fig. 2. Variation in egg dimensions with clutch size.

between early and late clutches ($t = 3.33$, $df = 74$, $p < 0.05$; $t = 2.09$, $df = 74$, $p < 0.05$, respectively).

Egg dimensions (length, breadth and volume, respectively) did not depend on the clutch size ($F_{4,69} = 2.95$, ns; $F_{4,69} = 0.84$, ns; $F_{4,69} = 1.10$, ns), but the largest eggs were found in clutches with six and eight eggs (Fig. 2).

The sixth eggs were slightly larger than the other ones (Fig. 3), but we did not find any influence of the laying sequence on the egg size in clutches of the same size. The traits of eggs (length, breadth and volume, respectively) in the sequences were not significantly concordant in clutches with 6 eggs (Kendall's coefficient of concordance $W = 0.07$, $W = 0.10$, $W = 0.06$) and with 7 eggs ($W = 0.08$, $W = 0.07$, $W = 0.09$).

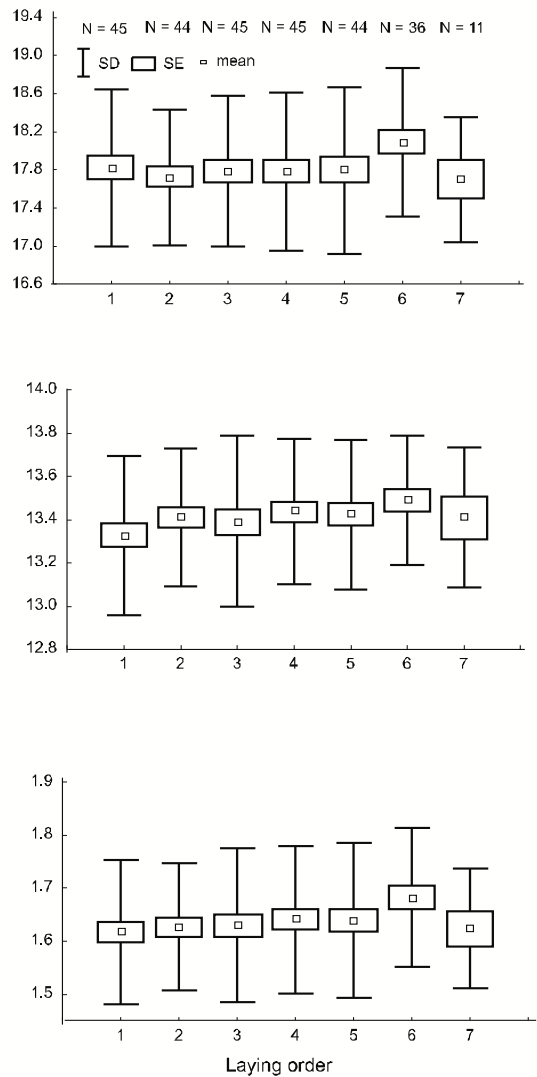


Fig. 3. Variation in egg dimensions with laying sequence.

Table 4. Correlation coefficient between female body size and egg dimensions. *— $p < 0.05$.

	Wing length n = 50	Length of tarsus n = 48	Weight n = 44
Length	0.07	0.31*	0.26
Breadth	0.14	0.30*	0.35*
Volume	0.10	0.35*	0.36*

Tarsus length and weight of female were positively correlated with eggs dimensions, but the relation with wing length was non-significant (Table 4). Eggs laid by older females were slightly bigger (Table 5) but differences between egg size in one-year old females and older ones were not significant ($t = -0.19$, ns; $t = -0.78$, ns; $t = -0.56$, ns).

Table 5. Egg dimensions of one-year (n = 10) and older (n = 37) females.

	Mean \pm SD	Min–Max
Lenght (mm)		
one-year	17.92 \pm 0.92	16.70–19.30
older	17.97 \pm 0.62	16.76–19.24
Breadth (mm)		
one-year	13.40 \pm 0.37	12.78–13.81
older	13.47 \pm 0.31	12.83–14.22
Volume (mm ³)		
one-year	1.64 \pm 0.15	1.40–1.83
older	1.67 \pm 0.12	1.51–1.94

DISCUSSION

The studied eggs of the Collared Flycatcher from the Białowieża Forest were slightly larger than noted in Czech Republic and Hungary, but smaller than in the Niepołomice Forest and in Slovakia (Glutz et al. 1993). Eggs were very similar to those originating from Russia (Peklo 1987). This pattern could not be explained by the geographic variation and probably main factors of the variability are local conditions. In other species it was demonstrated an egg size increase from the south to the north (Järvinen & Väisänen 1983, Järvinen & Pryl 1989).

Similarly to other authors it was not found any differences in eggs size between years (Ojanen et al. 1979, Järvinen & Väisänen 1983, Järvinen & Pryl 1989, Potti 1993, Nager & Zandt 1994). This indicated stable environmental conditions (i.e. the abundance of food) or no effect from this factor on egg size variation. This interpretation is supported by lack of significant differences in densities of caterpillars in the Białowieża National Park during the study period (P. Rowiński, T. Wesołowski — unpublished data).

The results above generally support conclusions from other papers about the relation between the variation of egg size and female size. Similarly as in the best known species of cavity nesters, the Pied Flycatcher *Ficedula hypoleuca* and the Great Tit *Parus major* (Ojanen et al. 1979, Järvinen 1991, Potti 1993, Nager & Zandt 1994), in the Collared Flycatcher's egg size was positively correlated with female size. It is difficult to explain this association with only one kind of factor (genetic or environmental). The increase in egg size with the tarsus length of female may be determined by environmental factors (Alatalo et al. 1990) or by genetic ones — the same genes may

affect the tarsus length as well as eggs' size (Potti 1993). However, the relationship between egg size and female body weight probably depends on abundance of food (territory quality) and ability of female to find a suitable amount of food. This ability may be affected not only by heritable factors but also by age (or experience) of female (Stuchbury & Robertson 1987, Burger 1988, Pyle et al. 1991). The lack of relationship between egg size and wing length was mentioned in other papers (Järvinen & Pryl 1989, Cichoń 1997). This fact pointed at other factors influencing wing length in addition to those connected with genes and conditions in the breeding area.

Environmental factors such as food abundance and temperature are closely related and it is difficult to analyse them separately. Experiments with manipulations of food abundance showed clearly the dependence of egg size on this factor (Arcese & Smith 1988, Boutin 1990). However, temperature can influence egg size indirectly by regulation of leaf development and abundance of food (Slagsvold 1976).

Our results show that early breeders laid larger eggs than later ones. It is probably associated with the age (experience) or the quality of female and with environmental conditions. In the Białowieża Forest older females of the Collared Flycatcher laid slightly larger eggs than one-year old ones, but differences were statistically not significant. In many papers the influence of female age on the beginning of the egg laying period was described (Perrins 1970, Wiggins et al. 1994, Verhulst et al. 1995, Sanz 1997). However, other authors reported a lack of influence of female age on egg size and indicated differences in the quality of female or of breeding territory as main factors of the described variation (Ojanen et al. 1979, Potti 1993, Nager & Zandt 1994).

The results of present study did not clearly show an influence of clutch size on dimensions of eggs. Järvinen & Pryl (1989) observed in Great Tits dependence between egg size and clutch size, where eggs were largest in nests with 9 eggs, while in clutches with a higher number of eggs smaller ones were found. Such conclusions were reached also by Potti (1993), who carried out investigations on the Pied Flycatcher and on many other bird species (Blackburn 1991). However, Potti (1993) reported that some females of the Pied Flycatcher in years of food abundance laid bigger eggs in larger clutches. This phenomenon may be explained by the trade-off between costs and advantages of laying big eggs in small clutches or

of laying small eggs in large clutches. Large eggs give many advantages, including greater probability of hatching a nestling, higher survival of nestling and higher probability of leaving the nest (Järvinen & Ylimaunu 1984, Williams 1994, Perrins 1996). On the other hand, production of larger eggs demands more nutrients, which is also associated with higher costs of incubation and of feeding larger nestling (Perrins 1996).

There was not found any influence of the laying sequence on egg dimensions. In the Great Tit and in many other species (Ojanen et al. 1981, Bańbura & Ziełiński 1995), as in the present work, such a relationship was not evident. However, in the Pied Flycatcher and in the Collared Flycatcher it was reported that first eggs were smaller than later ones (Potti 1993, Cichoń 1997). On the contrary, in the Black Redstart *Phoenicurus ochruros* and in many other species it was observed that first eggs were larger than next ones (Ojanen et al. 1981, Robertson & Cooke 1993). Many authors reflected over reasons of the variability of eggs inside a clutch. Among many factors, they pointed most often at the variation of environmental conditions, such as temperature and the availability of food (Ojanen et al. 1981, Järvinen & Pyl 1989, Slagsvold & Lifjeld 1989, Magrath 1992). These factors had greater effect on eggs laid later. Variation in egg size affects also size of nestling (Williams 1994, Perrins 1996), which can be an adaptation to changeable of food conditions and allows for the optimization of the parent effort and breeding success (Lack 1954, Slagsvold et al. 1984, Williams 1994, Perrins 1996).

In conclusion, egg size of the Collared Flycatcher in the Białowieża Forest seems to be influenced more by characteristics of female than by environmental conditions.

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[Zmienność wielkości jaj muchołówki białoszyjej w Puszczy Białowieskiej]

Najczęściej wskazuje się na dwie grupy czynników wpływających na zmienność wielkości ptasich jaj: cechy samicy i czynniki środowiskowe. Celem pracy było określenie wpływu cech samicy (wieku, parametrów biometrycznych), wielkości i terminu rozpoczęcia lęgu oraz kolejności składania na wielkość jaj muchołówki białoszyjej.

Badania prowadzono w latach 1997–1999, na powierzchni grądowej Puszczy Białowieskiej z użyciem skrzynek lęgowych. Ogółem zmierzono 445 jaj z 82 lęgów. Średnia długość jaj wyniosła 17.82 ± 0.80 mm, szerokość 13.45 ± 0.37 mm, objętość 1.65 ± 0.14 cm³ (Tab. 1). Wymiary jaj były pozytywnie ze sobą skorelowane ($r = 0.50$, $p < 0.01$, $n = 75$; Fig. 1). Nie stwierdzono różnic w rozmiarach jaj między sezonami (Tab. 2). Samice przystępujące wcześniej do lęgów składały jaja dłuższe i o większej objętości niż przystępujące później (Tab. 3). Rozmiary jaj nie zależały od wielkości lęgu, ale były one nieco większe w lęgach złożonych z 6 i 8 jaj (Fig. 2). Nie stwierdzono istotnego wpływu kolejności złożenia jaja na jego rozmiary (Fig. 3). Rozmiary jaj były pozytywnie skorelowane z długością skoku i ciężarem samicy, natomiast nie stwierdzono wpływu długości skrzydła na cechy jaj (Tab. 4). Jaja złożone przez starsze samice (w trzecim i kolejnych latach życia) były nieznacznie większe od jaj młodych samic (w drugim roku życia — Tab. 5).