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Egg size Variation in the Collared Flycatcher (*Ficedula albicollis* Temminck, 1815)

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This work aims to examine the factors influencing variation of the Collared Flycatcher's egg size at the southern borders of the distribution of deciduous forests (Homil'shanski Lisy National Park, Ukraine). In total, data on 298 clutches and 1971 eggs of the Collared Flycatcher in artificial nest-boxes for 2006–2011 and 2013–2021 were used for analyses. As the meteorological indicators we used the temperature, a number of days with rainfall during the 1st decade of May; and humidity indices. All statistical analyses were performed with R statistical software version 4.4.2, A Shapiro–Wilk test for normality revealed that data were not normally distributed. Therefore, for further analysis, we used the Kruskal – Wallis test and Dunn test as well as Permutational Analysis of Variance (PERMANOVA) of the distance matrix. The vegan package was used for analysis. We analyzed the effects of meteorological indicators on egg size using generalized additive models. Statistical analyses were performed using *mgcv* packages.

In the studied subpopulation, the average egg length tends to decrease in the period from 2006 to 2021 and is slightly dependent on clutch size and the decade of first-egg laying. The seasons with the smallest egg sizes in the studied subpopulation spanned 2014 - 2018; later on, there was an increase in egg diameter towards the usual size for this subpopulation. The consistently small diameter of the eggs can be assumed to indicate that during this period, young females predominated in the studied subpopulation.

In general, the size of the eggs in the last season was similar and even somewhat larger (especially in length) to those obtained in the Sumy region of Ukraine, and in certain years exceeded the indicators of the eggs of flycatchers from the Bialowieza Forest. It can be assumed that larger eggs are laid by females under optimal conditions within the species' range; as they move towards the borders of the range to the north and east, the morphometric parameters may decrease due to the decline in the quality (abundance of food) of the environment.

The analysis of the repeatability of egg sizes in the same female should answer the question of whether the size of the egg is an individual's characteristics of females. However, we did not receive a definitive answer.

The humidity of the pre-laying decade has a significant negative impact on the morphological parameters. The humidity during the egg-laying decade has a positive influence, while to a lesser extent, the temperature of the decade prior to egg-laying also positively affects the length of the eggs. The temperature of the previous decade and the number of rainy days play a minor role. At the same time, there is an optimum for these indicators, beyond which the effect of their influence on the size of the eggs changes to the opposite. In the studied area, the length and diameter of eggs from early and late did not differ significantly. Only in certain years, the differences in length, diameter, and volume are significant.

The variation of the morphological parameters are an integrated response to the instability of environmental parameters. One of the reasons for high variability in egg sizes may be humidity. The size of the eggs itself cannot be explained by the climatic conditions of the current year. They are an integrated indicator of the female's maturity and the nutritional conditions of the season.

Keywords: *Ficedula albicollis, egg size, weather condition*

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Introduction

The size and number of eggs are important components of reproductive strategies, with implications for the offspring and parental fitness (Guo et al.,2022). Egg size is a useful metric for maternal investment and offspring quality (Mark et al., 2021).

Variation in egg size among individuals is caused by a combination of genetic and environmental factors differences. Variation in egg size within an individual among years is caused by temporary environmental differences between reproductive attempts (Falconer, 1989). Egg size is a particularly important life-history trait mediating maternal influences on the offspring phenotype ("maternal effect" (Potti, 1999)). It is believed that females can vary the size of their investment in egg-laying depending on environmental conditions, their own reproductive state, and the quality of the partner (Hargitai et al., 2005). The size of the eggs a female lays is usually regarded as an indicator of the female's or territory's quality (Hörak et al. 1997, Silva et al. 2007). Many authors have discussed the dependence of egg size on their rank in the clutch - eggs laid first are larger, while the last ones may be smaller due to poorer nutrition (Jarvinen et al., 1986), the age of the female (Jarvinen et al., 1989; Mitrus, 2001), and heredity (Ojanen, 1983). Later, no effect of the sequence of laying on the egg size was found. Eggs laid by older females are slightly larger, but the differences between egg sizes in one-year-old females of different ages are negligible. It was noted that the sizes of the eggs positively correlated with the leg length and weight of the female (Mitrus et al, 2001).

The reasons for the variability in egg sizes can be grouped as follows:

— the change in egg size in one individual over different years is caused by environmental conditions during different breeding seasons (Falconer, 1989), related to the availability and accessibility of food; in turn, the availability and accessibility of food depend on the local climatic conditions of the year (including location within the range), as well as on the experience of the female (age) and body size (Cristian, 2002; Hargitai et al., 2005);

— the influence of the female's heredity or age (which determines her physical condition); the last group clearly includes the long-term effects of parasitic infections on the size of eggs, offspring, and the subsequent condition of young flycatchers; the long-term impact of parasitic infection is described (Potti, 2008).

Thus, the presence and availability of food are ones of the main factors determining the physical condition of birds and, ultimately, the production of viable offspring. Climate change affects the quantity, quality, timing, and availability of food resources, which can be reflected in the indicators of the reproductive cycle (egg morphology, timing, and duration of laying, etc.).

Global climate change has been shown to cause variable shifts in phenology of different animals (Adamik et al., 2007). As response to climate change, the shift in phenological stages to earlier dates, changes in phenological phases duration (Bauer et al., 2010) have been indicated as well as changes in clutch sizes (Laaksonen et al., 2006) and nesting success (Slobodník et al., 2013). Shifts in the seasonal timing of species may differ depending on the trophic level, and, as a result, the phenology of predators may be out of sync with phenology of their prey, or vice versa - the early entry of offspring in predators will increase the impact on the survival of the offspring of hollow-nesting birds.

The effect of climate on reproduction and morphology have been also described (Przybyo et al., 2000). Autors analyzing cross-correlations between the winter NAO index and reproduction and morphological traits. Such idicators as laying date, clutch size, edging success, number of recruits produced, tarsus and wing length are used.

Seasonal temperature variation affects changes in the diet of flycatchers differently (Burger et al., 2012). The development of spring phenology could shift some food sources necessary for egg laying, which leads to later egg laying and smaller clutches (Laaksonen et al., 2006).

In general, increase in air temperature clearly affects duration of the phenological phases: the date of the first setting and the average date of setting. However, this change does not appear to have resulted in incorrect timing in the trophic food chain (Bauer et al., 2010).

Changes in local climate conditions may also affect the competition for resources between resident and migratory bird species by altering their breeding intervals or changing their population density (Ahola et al., 2007). Spring temperature has stronger effect on the breeding phenology of the resident species (tits) than migrants (flycatchers). However, density of the resident species increased after warm winters, having affected the mortality of the migratory species as a result of the increased competition (Samplonius, Both, 2019).

Climatic conditions played a key role in the evolution of passerine egg shape (Duusmaa et al., 2018). The trend towards decreasing egg diameter and volume due to inconsistent reproduction phenology linked to climate warming was noted as early as 2008. The reason was the mismatch of phenological dates of food abundance for optimal egg formation, which affects the condition of the female and leads to a smaller average egg size (Potti, 2008). In addition, environmental conditions during egg formation may influence conditions for embryonic development. It was noted that the magnitude of hatching deviation increased with the number of cool days and heavily rainy days (Hargitai et al., 2009).

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The dependence of egg parameters on climatic factors has been demonstrated for the Pied flycatcher (*Ficedula hypoleuca)* in Łódź, central Poland: a tendency to decrease the length, width, and volume of eggs over a period of 10 years has been shown (Skwarska et al., 2015).

This work aimed to examine factors influencing variation of the Collared flycatcher's egg size at the southern borders of the distribution of the deciduous forests.

Materials & Methods

Study site and study species

We collected data between 2005 and 2021 in the Homil'shanski Lisy National Park, Ukraine (centered at N 49°37′31.1″ N, 36°19′ 28.7″ E). The studied plots (9 and 17.9 ha) are located in the south of the Forest-Steppe of Left-Bank Ukraine, in the upland maple-linden oak forest (Acereto-Tilieto-Querceta graminosa) consisting of Common Oak *Quercus robur* (age of 40-150 years), Small-leaved Lime *Tilia cordata*, and Field Maple *Acer campestre* (Gorelova, Alekhin, 2002).

The 100 wooden nest boxes arranged in a grid system with an average distance of 50 m are mainly used by the Collared Flycatcher and to a lesser extent by the Great Tit (*Parus major*) and Blue Tit (*Cyanistes caeruleus*). The first Collared Flycatchers usually arrived to the Homil'shanski Lisy National Park during the 9-19 April; (mean = April 15) in different years. Within a clutch 4–9 eggs (but typically 5–7) are laid during the consecutive days, one egg per day, and laying gaps are extremely rare in our population (Atemasov et al., 2024). Females raise only one brood within a reproductive season, but re-nesting events are possible in the case of previous failures. In the maple-lime-oak forest in the left-bank the Forest-Steppe border of Ukraine that we studied, the Collared Flycatcher is one of the four dominant species in the breeding bird's communities – 396 pairs/sq.km (Atemasov et al., 2011).

Eggs were measured (length and width) using sliding callipers to the nearest 0.1 mm. Variation of such indicators as length, maximum diameter, and volume have been analyzed. Coefficients of variation have been calculated for such indicators as length (L), maximum diameter (d) of eggs in clutches of different sizes (Paevsky, 1985). To calculate egg volume, the formula: $V = 0.51 \times L$ (length) $\times d^2$ (diameter) was used, following Mijand (1988).

Clutches were divided into early and late ones according to the median date of laying the first egg. The repeated clutches (clutches created 20 days after the median of the laying period (by Wesołowski, 1985)) were excluded from the analysis.

In total, data on 298 clutches and 1971 eggs of the Collared Flycatcher in artificial nest-boxes for 2006–2011 and 2013–2021 were used for analysis.

Meteorological indices:

The following meteorological indices were calculated for each clutch:

— the sum of the effective average daily temperatures at the start of the laying - Σ FLD

— the sum of the effective daily temperatures for the 30 day before the start of laying - Σ 30 FLD;

— the sum of the effective daily temperatures for the 5 day before the start of laying - Σ 5;

— a number of days with rainfall for the 1st decade of May - MayIRain;

— the average temperature of the previous decade -T prev dek;

— the average temperature of the current decade - T actdek;

— the average air humidity index of previous decades - F prev dek

— the average air humidity index of current decades - F act dek

Data on average daily temperatures were obtained from the archive of meteorological data for Kharkiv and Zmiiv (Kharkiv Region, 7 km from the study area) for 2006–2011 and 2013-2021.

Statistical analyses

All statistical analyses were performed with R statistical software version 4.4.2 (R Core Team, 2024).

Shapiro–Wilk test for normality revealed that data were not normally distributed. Therefore, for further analyses, we used the Kruskal–Wallis test and Dunn test as well as Permutational Analysis of Variance (PERMANOVA) of the distance matrix. The *vegan* package (Oksanen et al., 2025) was used for analysis.

We analyzed the effects of meteorological indicators on the egg size using generalized additive models (GAM, Wood, 2006; Zuur et al., 2009). Statistical analyses were performed using *mgcv* package (Wood, 2006).

The systematics is provided according to IOC WORLD BIRD LIST (14.2). Birds were ringed in nests with standard aluminum rings of series A and B, provided by the Ukrainian Ringing Center (Kyiv). Data on re-encounters of 5 females marked in nests in 2007-2008, 2013-2014, 2016-2017, and 2017-2018 allowed for the analysis of individual characteristics of egg size.

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Results

Measurements of 1971 eggs from 298 clutches were taken in 2006–2011 and 2013–2021 (Tables 1, 2, S1). Results of the Kruskal–Wallis test showed that egg dimensions (length, diameter, and volume) differed significantly between years, egg laying period (decade) and clutch size (Fig. 1-3). Values of effect

Table 1. Annual variation in the egg dimensions. N — number of eggs

Year	N	Mean ± SE	Min – Max	Cv
		Lenght (mm)		
2006	74	18.03±0.65	16.60 - 19.40	3.60
2007	225	18.01±0.73	16.10 - 20.20	4.03
2008	222	18.14±0.66	16.50 - 20.00	3.64
2009	219	18.13±0.71	16.10- 20.10	3.94
2010	282	18.16±0.72	16.30 - 20.00	3.96
2011	215	18.17±0.81	15.90 - 20.10	4.48
2013	82	17.81±0.75	15.96 - 19.49	4.24
2014	130	17.59±0.74	15.00 - 19.50	4.20
2015	89	17.75±0.53	16.05 - 19.02	3.52
2016	122	17.65±0.92	15.23 - 19.92	5.20
2017	87	17.65±0.74	16.46 - 19.55	4.16
2018	32	17.62±0.54	16.07 - 18.72	3.05
2019	65	18.15±0.81	16.58 - 20.51	4.48
2020	58	17.89±0.65	16.56 - 19.42	3.63
2021	69	17.96±0.88	15.27 - 20.02	4.91
		Breadth (mm)		
2006	74	13.52±0.54	12.50-15.10	4.02
2007	225	13.38±0.42	12.00-14.30	3.18
2008	222	13.28±0.43	12.10-14.20	3.22
2009	219	13.46±0.44	12.00-14.20	3.24
2010	282	13.47±0.47	12.00-14.10	3.47
2011	215	13.43±0.48	12.00-14.70	3.56
2013	82	13.35±0.34	12.55-14.10	2.54
2014	130	13.06±0.27	12.20 - 13.90	2.06
2015	89	13.02±0.63	11.15 - 14.07	4.85
2016	122	13.31±0.46	12.00 - 14.23	3.47
2017	87	13.11±0.46	12.12 - 14.53	3.51
2018	32	13.06±0.30	12.40 - 13.85	2.33
2019	65	13.58±0.35	12.86 - 14.64	2.60
2020	58	13.42±0.51	12.53 - 14.50	3.81
2021	69	13.63±0.51	12.43 - 14.80	3.72
		Volume (cm^3)		
2006	74	1685.72±177.49	1416.93-2168.78	10.53
2007	225	1645.69±139.35	1292.54-2019.19	8.47
2008	222	1635.26±139.05	1242.72-1943.61	8.50
2009	219	1677.75±136.16	1290.94-1988.17	8.12
2010	282	1684.55±144.16	1233.79-2157.30	8.56
2011	222	1675.09±158.28	1175.04 - 1999.2	9.45
2013	82	1630.97 ±122.92	1386.09 - 2041.47	7.54
2014	130	1531.46±107.23	1222.61 - 1812.48	7.00
2015	89	1555.14±167.89	1096.66 - 1916.35	10.80
2016	122	1599.48 ±169.52	1142.73 - 1968.51	10.60
2017	87	1550.05±139.18	1295.91 - 1971.25	8.98
2018	31	1534.07±96.75	1365.96 - 1805.93	6.31
2019	65	1708.69±143.32	1427.32 - 2097.03	8.39
2020	57	1645.7±142.9	1330.20 - 2194.20	8.68
2021	68	1707.51±183.60	1287.11 - 2220.11	10.75

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size, which provide information about the magnitude of the differences between groups are presented in Table 3. The effect size for all dimensions by years is moderate, by decade and clutch size is small.

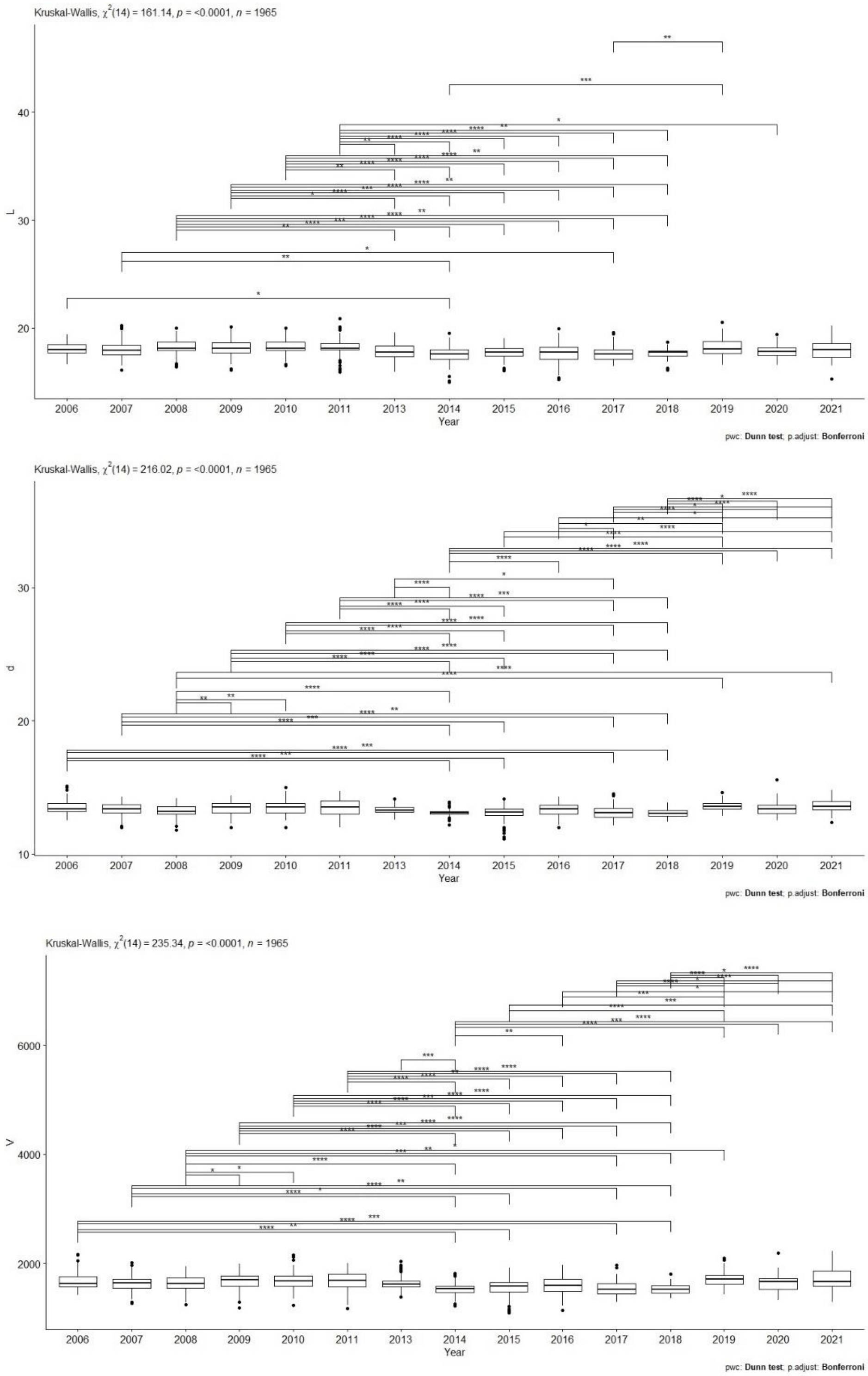

Fig. 1. Variation in egg dimensions by years

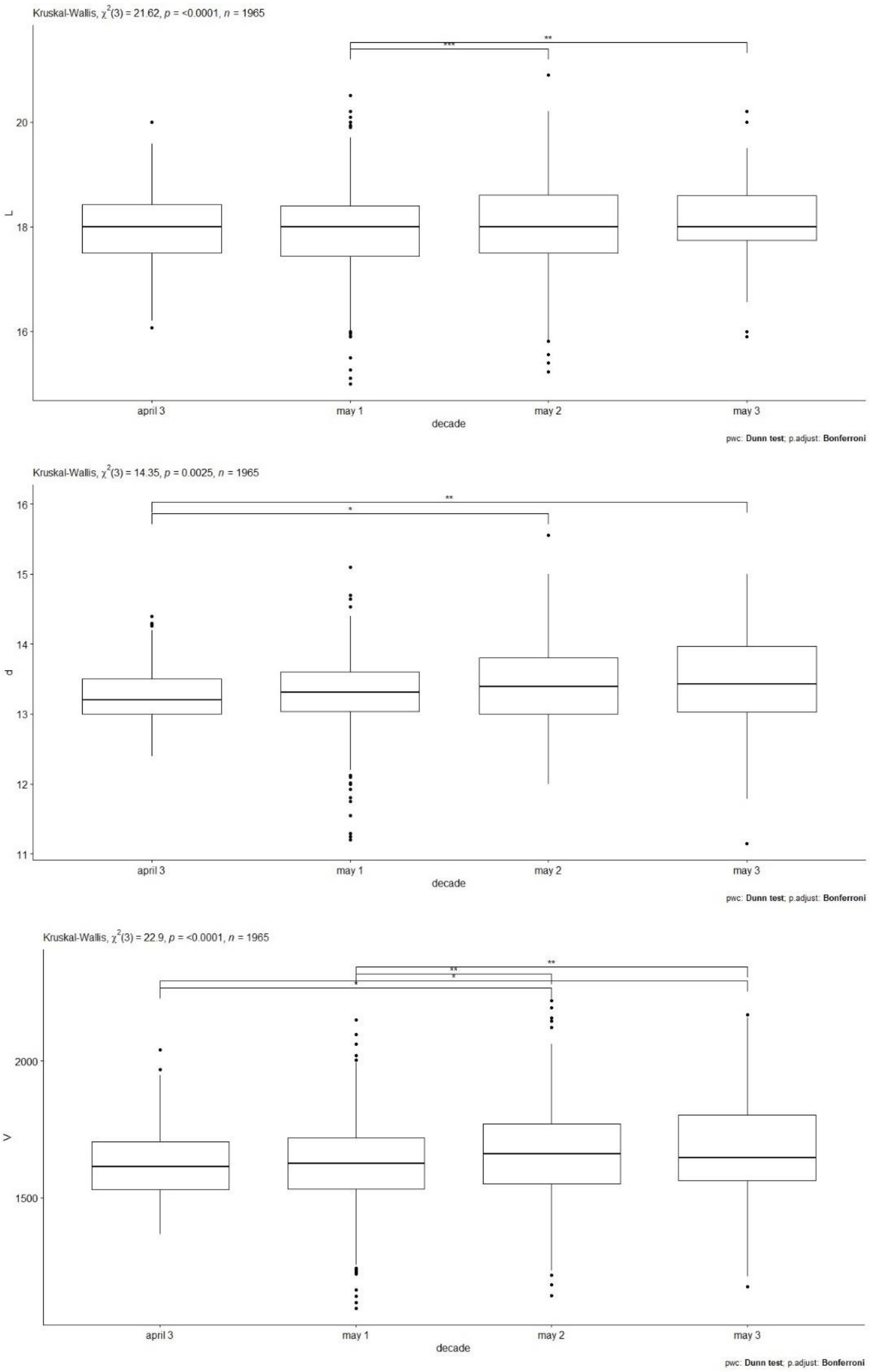

Fig. 2. Variation in egg dimensions with egg laying period (decade)

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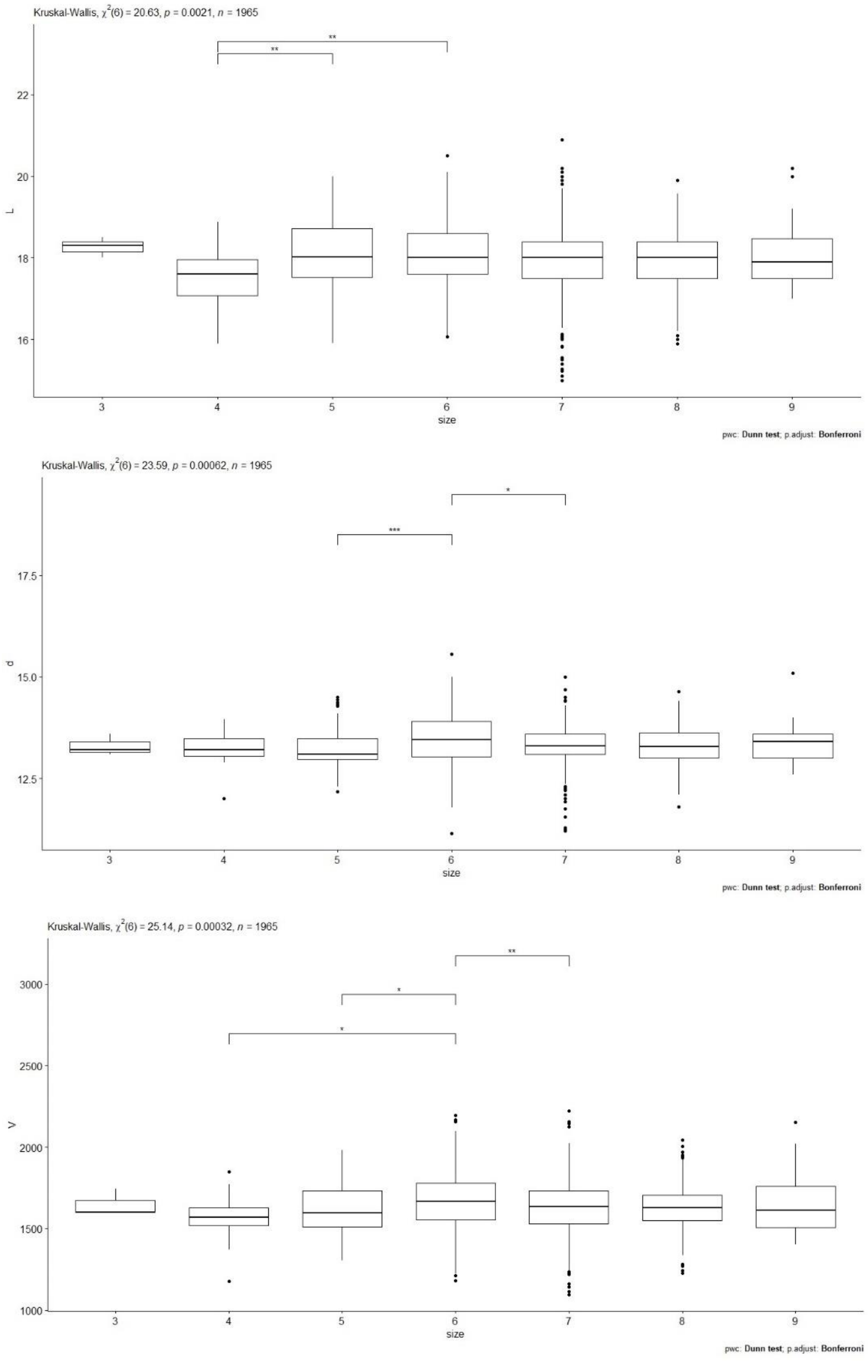

Fig. 3. Variation in egg dimensions with clutch size

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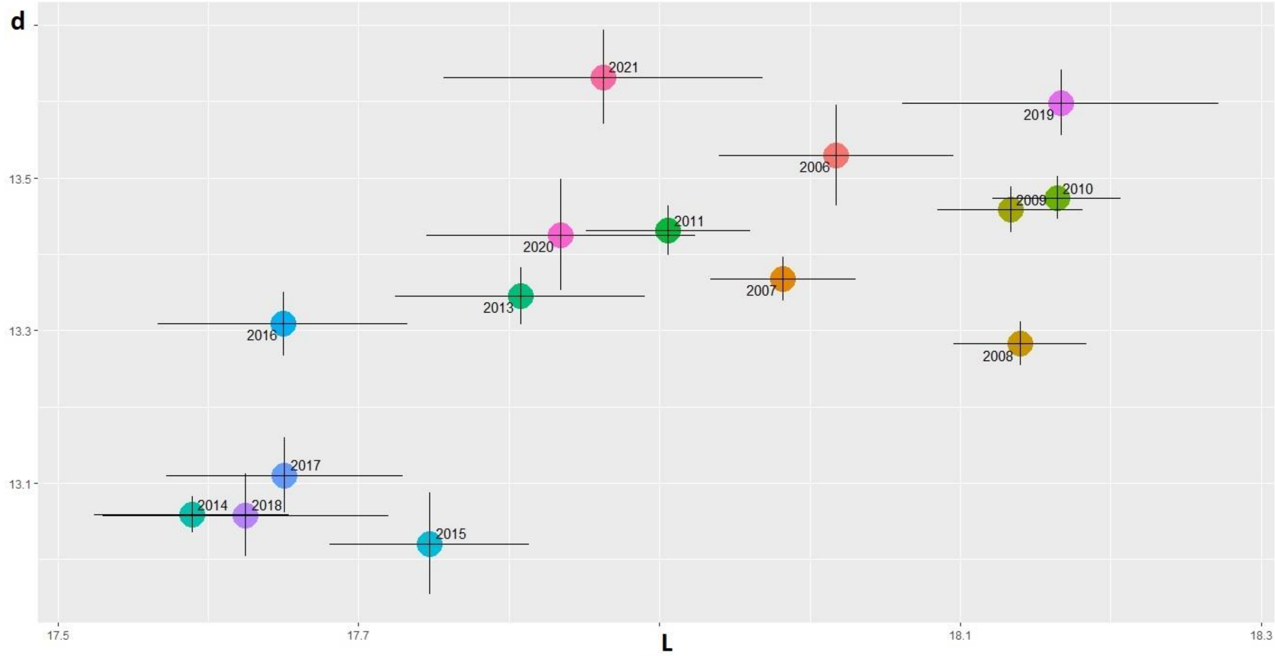

Fig. 4. Distribution of average length and diameter parameters of eggs in the studied subpopulation over the years

Table 2. Variation of egg (n = 1971) dimensions (pooled data)

	Mean ± SE	Min – Max
Length (mm)	17.99 ± 0.47	15.0 - 20.51
Breadth (mm)	13.33 ± 0.86	11.20 - 15.56
Volume (mm^3)	1638.23 ± 275.09	1140.66 - 2220.11

Table 3. Effect size (Dunn test) of the years, egg laying period (decade) and clutch size on egg dimensions

	by years	by decade	by clutch size
Length	0.0755 (moderate)	0.00950 (small)	0.00747 (small)
Breadth	0.1040 (moderate)	0.00579 (small)	0.00898 (small)
Volume	0.1140 (moderate)	0.01010 (small)	0.00978 (small)

Overall, the number of clutches in 2013-2021 was significantly lower, with smaller average size. The general decrease in morphological indicators in the clutches of 2013-2021, especially in 2014-2018, is noteworthy. At the same time, the clutches from 2019 have fairly similar morphological indicators to the numerous clutches from 2006-2011. A separate group includes clutches from 2011, 2013, and 2020-2021 - with an average egg length, their diameter corresponds to that of eggs from clutches from 2006-2010. Overall, eggs from clutches from 2014-15 and 2017-2018 are distinguished by having minimal length and diameter measurements. In other respects, the diameter of eggs from all other clutches remains quite stable, while the length is the most variable and is maximum in clutches from 2008-2010 and 2019. No linear dependence is observed. At the same time, eggs with the maximum diameter are characteristic of the clutches from the years 2006, 2019, and 2021 (Fig. 4). It can be assumed that this is related to the body size of the females nesting in the specified years.

The results of PERMANOVA showed statistical significance of year, egg laying period (decade), and clutch size, as well as the effect of their interactions on egg dimensions (Table 4).

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Table 4. The statistical significance of the influence of various factors on egg dimensions

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	Signif.
Year	14	135.20	9.6571	16.4766	0.08469	0.001	***
decade	3	9.71	3.2369	5.5226	0.00608	0.001	***
clutch_size	5	22.79	4.5589	7.7781	0.01428	0.001	***
Year:decade	27	108.42	4.0155	6.8511	0.06792	0.001	***
Year:clutch_size	41	153.06	3.7333	6.3695	0.09588	0.001	***
decade:clutch_size	8	30.78	3.8478	6.5649	0.01928	0.001	***
Year:decade:clutch_size	14	52.64	3.7603	6.4156	0.03298	0.001	***
Residuals	1849	1083.72	0.5861		0.67888		
Total	1961	1596.34			1.00000		

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Local weather conditions

Since the reproductive conditions of females during the egg-laying period are mainly determined by the availability and accessibility of food, which in turn depends on temperature and humidity, we have evaluated the dynamics of air temperature and humidity during March, April, and May - in the pre-reproductive and main egg-laying periods (according to data from different years - from April 23 to June 1). The associated analysis of the morphological parameters of the eggs and the climatic characteristics of the season revealed the following patterns (Fig. 5 a-c, Tab. S3):

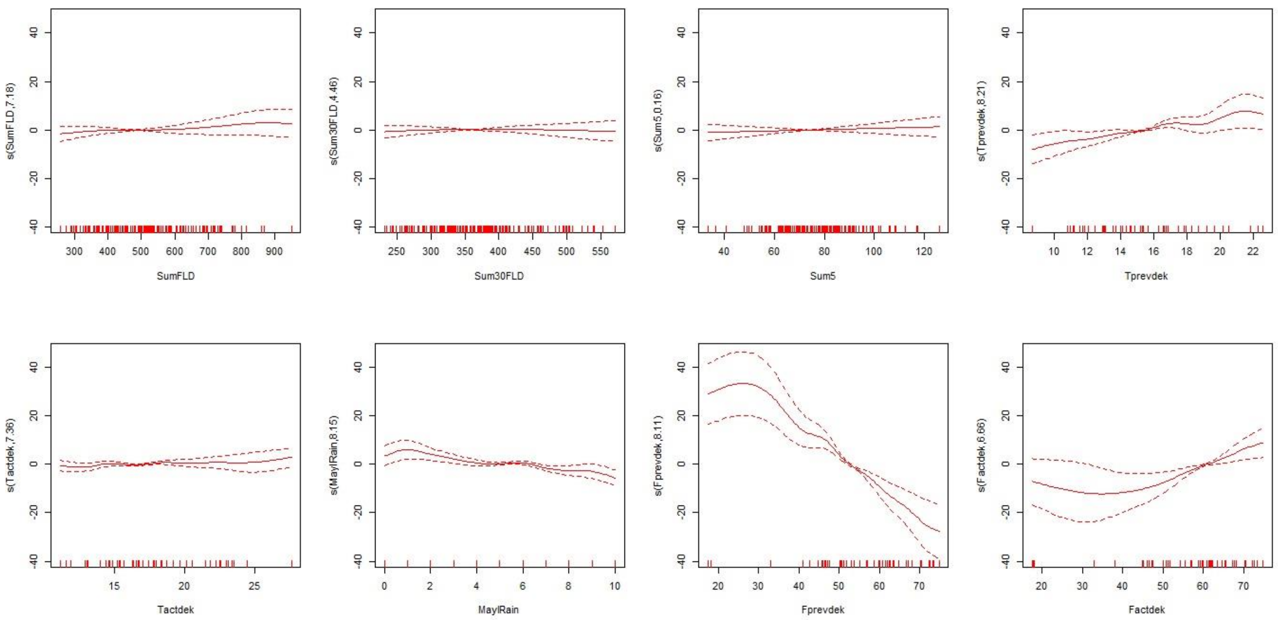

Fig. 5 a. Length (L)

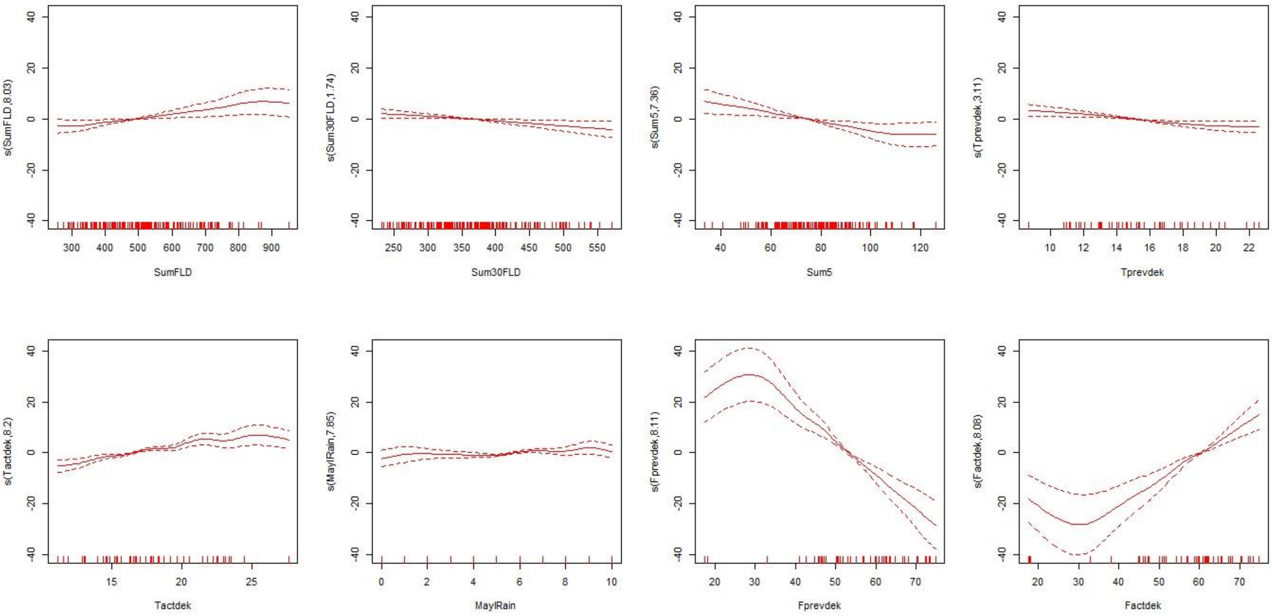

Fig. 5 b. Breadth (d)

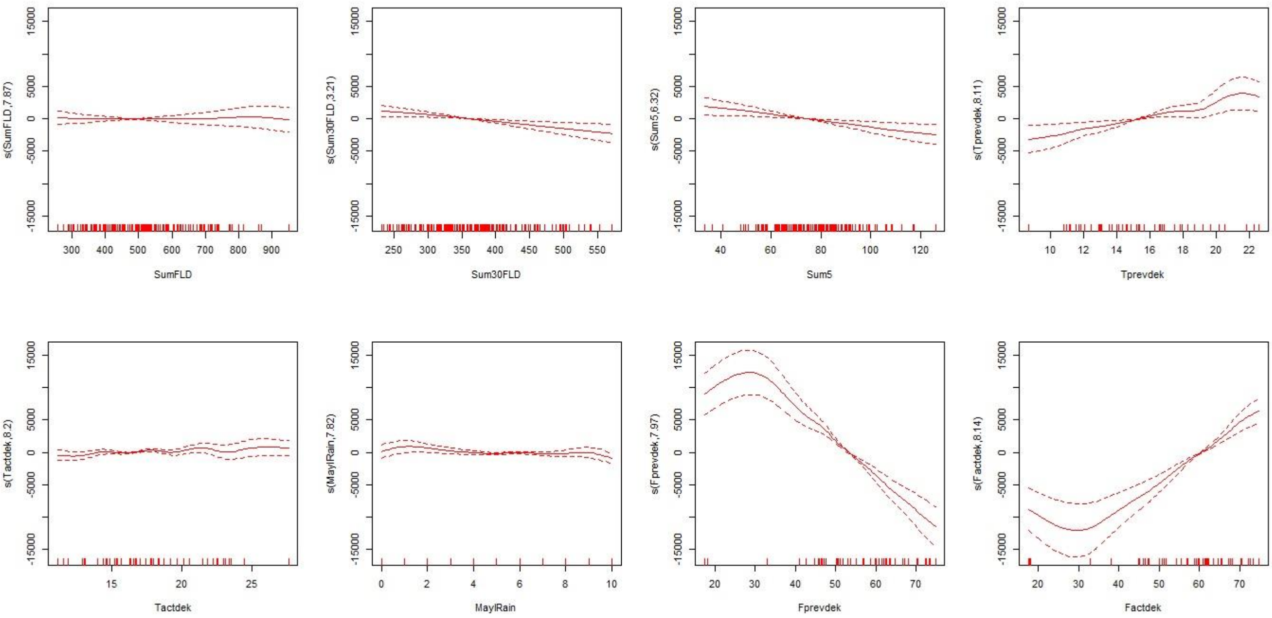

Figure 5 c. Volume

Figure 5 a-c. Response shapes of meteorological indicators in the GAM model for egg dimensions, (a) – length, (b) – breadth, (c) – volume. The dashed lines are approximate 95% point-wise confidence intervals; tick marks show the location of observations along the variable range; y-axes represent the effect of respective variable; s represents smooth term of GAM

The analysis of the influence of local weather conditions on the morphological parameters of eggs revealed significant components. These are the relative humidity of the air during the pre-laying period and during the egg-laying period. To a lesser extent, the air temperature during these periods is significant, and the number of rainy days is even less significant. (Fig. 5 a-c).

Early and late clutch

In certain years, early clutches significantly differed in diameter (2006, 2018), length and diameter (2007, 2021), and length (2009, 2016). Accordingly, the volume of eggs in these years also significantly distinguished early clutches from late ones (Tab. 5). In 2008 and 2019, there were no late clutches.

Table 5. Oomorphological parameters of early and late clutch in different years

Year	L		significance	d		significance	V		significance
	early	late		early	late		early	late	
2006	18.00± 0.59	18.05± 0.70	ns	13.31± 0.47	13.69± 0.55	**	1628.94± 147.78	1731.41± 187.68	**
2007	17.97± 0.70	18.57± 0.94	*	13.36± 0.43	13.67± 0.19	**	1637.28± 136.05	1772.34± 131.05	**
2009	18.18± 0.68	17.76± 0.86	*	13.48± 0.42	13.30± 0.51	ns	1686.75± 128.12	1607.89± 175.08	*
2010	18.13± 0.75	18.30± 0.56	ns	13.46± 0.47	13.52± 0.47	ns	1678.34± 142.94	1710.19± 147.66	ns
2011	18.15± 0.78	18.32± 1.07	ns	13.43± 0.47	13.42± 0.56	ns	1672.99± 148.34	1690.97± 222.51	ns
2013	17.85± 0.80	17.55± 0.33	ns	13.43± 0.34	13.42± 0.35	ns	1640.44± 125.35	1575.74± 93.79	ns
2014	17.58± 0.76	17.62± 0.60	ns	13.06± 0.27	13.04± 0.28	ns	1531.89± 110.12	1528.78± 89.78	ns
2015	17.83± 0.58	17.65± 0.67	ns	12.98± 0.67	13.07± 0.58	ns	1553.53± 185.75	1556.94± 147.58	ns
2016	17.61± 0.92	18.33± 0.70	*	13.32± 0.47	13.18± 0.28	ns	1598.20± 172.25	1624.24± 110.82	ns
2017	17.68± 0.66	17.57± 0.92	ns	13.17± 0.48	12.94± 0.37	ns	1567.0± 136.23	1502.90± 139.33	ns
2018	17.61± 0.58	17.69± 0.31	ns	13.10± 0.31	12.86± 0.15	*	1543.95± 102.43	1491.27± 53.54	ns
2020	17.90± 0.63	17.83± 0.75	ns	13.47± 0.53	13.19± 0.30	ns	1658.44± 144.63	1584.55± 122.77	ns
2021	17.42± 0.84	18.18± 0.81	**	13.15± 0.34	13.83± 0.43	****	1538.03± 102.11	1776.69± 163.72	****
Total	17.84± 0.24	17.95± 0.35	ns	13.28± 0.17	13.31± 0.30	ns	1610.44± 57.54	1627.22± 99.43	ns

ns – not significant, * - p<0.05, ** - p<0.005, **** - p<0,00005

Individuality: repeatability of egg sizes in the same females

We analyzed the sizes of the eggs in 5 individually marked females over 2 consecutive years (table 3). For 4 out of 5 birds, a decrease in egg length was observed in the subsequent clutch; the most consistent parameters were characteristic for 2 birds. For 2 out of 5 birds, the discrepancies were significantly larger. The sample may be too small to confirm or refute this hypothesis.

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Table 6. Individuality: repeatability of egg sizes in the same females

Fe-males	Year 1	L	d	Year 2	L	d	Mann-Whitney U test (L)	Effect size (L)	Mann-Whitney U test (d)	Effect size (d)
A	2007	19.8± 0.098	13.7± 0.063	2008	18.8± 0.084	13.5± 0.109	24; p=0.11; ns	-	23; p=0.163; ns	-
B	2007	17.8± 0.088	13.5± 0.047	2008	17.7± 0.159	13.6± 0.118	29.5; p=0.56; ns	-	19; p=0.519; ns	-
C	2013	17.4± 0.161	13.0± 0.054	2014	17.1± 0.067	13.0± 0.151	26; p=0.188; ns	-	15; p=0.742; ns	-
D	2016	17.5± 0.166	13.5± 0.055	2017	17.8± 0.105	12.8± 0.043	18; p=0.456; ns	-	49; p=0.00214; **	0.838; large
E	2017	18.1± 0.261	13.7± 0.146	2018	17.6± 0.261	13.4± 0.088	30; p=0.234; ns	-	36.5; p=0.0319; *	0.615; large

Discussion

Among the factors affecting egg size are mentioned:

— individual characteristics of female (for the Pied Flycatcher proven by Ojanen, 1983, for the Collared Flycatcher it remains controversial): the age of the female and female body weight;

— abundance of food (the quality of the territory) and the female's ability to find a suitable amount of food (Stuchbury et al., 1987; Burger, 1988; Pyle et al., 1991). This ability may depend not only on hereditary factors, but also on the age (or experience) of the female;

— local climate conditions as temperature, humidity (sufficient food supply during the egg-laying period) - usually have specific features in different years.

Each of these factors is connected with others. The latter can explain geographical and interannual variability.

Geographical variations in the egg size.

Some authors note the change in egg sizes at different geographical points of the overall range. In some species, it was demonstrated that egg size increases from the south to the north (Järvinen & Väisänen, 1983, Järvinen, Pryl, 1989). The effect of latitude on the correlation of egg size with clutch size has also been established: for example, egg size in the Pied Flycatcher was negatively correlated with clutch size between 40° and 51° N (Encabo et al., 2002).

The studied eggs of the Collared Flycatcher from the Białowieża Forest were slightly larger than noted in the Czech Republic and Hungary, but smaller than in the Niepołomice Forest and in Slovakia (Mitrus et al., 2001). The influence of the geographical component is probably indirect through the peculiarities of the climate in different parts of the rangewhich in turn may account for relatively larger or smaller egg sizes (possibly, this could also be related to year-to-year differences in egg sizes).

Analysis of literature data from the Ternopil region (Talposch et al., 1995), Sumy region (Knysh, 2003), Vinnytsia region (Seliverstov, 2008), and Bialowieza Forest (Mitrus et al., 2001) showed similarities in the length and diameter of eggs in the studied subpopulation with similar parameters from the oak forests of the Sumy region; length and diameter of the eggs were generally larger than those in the oak forests of Bialowieza Forest (Tab. 1 of the appendix). Thus, a slight increase in egg length has been shown from west to east.

The oological materials of the collections of A. V. Nosachenko from Cherkasy (Seliverstov, 2008) show similarities in the parameters of the eggs of the Collared Flycatcher with modern clutches from the Northeast and East of Ukraine (Atemasova et al., 2014; Knysh, 2003) despite a 100-year time interval. At the same time, these parameters have a large variation between the years (1922-1927), demonstrating both maximum and minimum parameters (Fig.6).

The geographical point of the Savalsky Forest is located 600 km to the northeast from the studied region and is characterized by low sizes (lower than those in the Bialowieza Forest, the clutches are similar in size).

Changes in egg size depending on geographical latitude and clutch size remain poorly studied. A clear negative correlation between egg size and clutch size along latitudinal gradients has not been confirmed (Guo et al., 2022).

Oomorphological parameters and variability (Cv) as indicators of stability of the environmental conditions

The authors previously showed a significant difference in the length and diameter of eggs in clutches of different sizes ($p<0.05$), i.e., with an increase in clutch size, the length and diameter of the eggs decrease (Атемасова и др., 2014). The same pattern was noted by Knysh (2003) and Talposh et al. (1995).

Interannual variations in egg sizes show a general trend of egg length decrease (a slight increase in 2019); the diameter fluctuates, decreasing in 2014 - 2018 (Tab. 1, Fig. 6). Therefore, it can be assumed that during this period, young females predominated in the studied subpopulation.

The influence of the year on egg size is moderate, however, it is greater than the influence of clutch size or the decade of egg laying (Tab. 3).

Lack of differences in egg size between years is considered by some authors to indicate stable environmental conditions (i.e., abundance of food) (Ojanen et al., 1979; Järvinen, Väisänen, 1983; Järvinen, Pryl, 1989; Potti, 1993; Nager, Zandt, 1994). High variability in egg size parameters instability of environmental conditions of the current breeding season conditions.

Under stable environmental conditions in Białowieża Forest, the egg sizes of the Collared Flycatcher were stable and both indicators (L and d) were positively correlated. It positively correlated with the clutch size also (Mitrus et al., 2001).

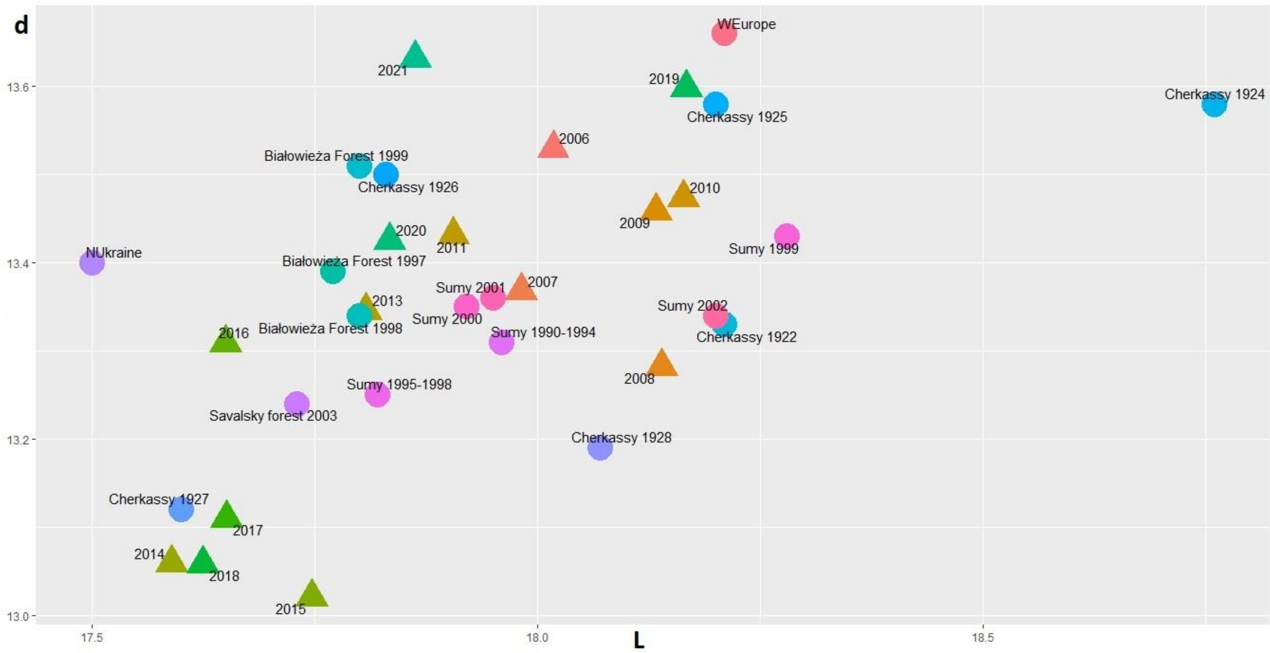

Fig. 6. Oomorphological parameters in various geographical zones and years (years points only - in our subpopulation)

The egg dimensions (length, diameter, and volume) differed significantly between years, egg laying period (decade) and clutch size (Figs. 1-3). Similarity in these parameters is noted between different years, sometimes quite distant from each other.(Fig. 6). Years with a minimal egg size in the studied subpopulation are highlighted (2014, 2015, 2017, and 2018). The 2016 clutches also have a small diameter. However, the length and diameter parameters are mostly larger than those reported in the literature for the Bialowieza Forest, the Savalsky Forest, and the Sumy region. The nests from Nosachenko's collection, gathered in the Cherkasy region between 1922 and 1927, show a large variation in parameters; however, they are few in number and rather indicate individual characteristics of the females.

The variability of length and diameter of eggs in clutches of various sizes in different years (Tab. S1) and average variation indicators by year are high in the studied subpopulation: in 2007, the coefficients of variation for egg length ranged from 3.56 to 5.76 for all size categories of clutches (Tab. S1). It can be assumed that this is a response to unstable environmental conditions. This year was characterized by a short spring period (from the transition from +5°C to +15°C took 10 days) and the shortest egg-laying period recorded over all observation years - 6 days. High variability indicators of egg length are characteristic for the 6th and 7th egg clutches (most common in the population) of 2016 (4.93 and 5.22 mm). It can be assumed that such high variability in length is a response to unstable environmental conditions.

Weather characteristics influence egg sizes

The local weather conditions in our study area determine the availability and abundance of food for insectivorous birds, and consequently - the condition of the female and her ability to lay sufficiently large eggs. Large eggs provide many advantages, including a greater likelihood of the chick hatching, higher chick survival rates, and a greater chance of successful fledging (Järvinen, Ylimaunu, 1984; Williams, 1994; Perrins, 1996).

In addition, egg production in birds requires a large part of the total energy budget, thus a clutch mass in some bird species can outweigh the body mass of the female (Li et al., 2003) and a decrease in air temperature (which requires additional energy to compensate for heat loss) can hinder the process of laying eggs.

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 regulating leaf development and abundance of food (Slagsvold, 1976). Sequentially laid eggs of small songbirds are built from the current income of resources and therefore can be subjected to different environmental influences on the short- and long-term perspectives (Skwarska et al., 2015). In adverse weather, aerial insect activity is reduced (Williams, 1961; Bryant, 1975; Peng et al., 1992), making it increasingly challenging to locate prey (Avery and Krebs, 1984), which is thought to reduce foraging efficiency (Cantar, Montgomerie, 1985).

Hargitai (2005) constated that egg size increased within clutches in years with a warm pre-laying period; while in years when the weather during that period was cold, there was no significant intra-clutch trend. Proximate considerations seem to explain the observed patterns of the intra-clutch egg-size variation; however, one cannot reject the adaptive explanation (Hargitai et al., 2005). Cristians (2002) believes that ambient temperature during egg formation generally explains less than 15% of the variation in egg size.

From the indicators we analyzed, following have significant influence on the oomorphological parameters: i) the humidity of the 10-days prelaying period (negatively), ii) humidity during the decade of egg laying (positively), and iii) to a lesser extent - the temperature of the 10-days pre-laying period (positively influences the length of the eggs). At the same time, there is an optimum for these indicators (humidity for pre-laying period 20-40 %), beyond which the effect of their influence on the size of the eggs changes to the opposite.

A number of researchers showed that temperature and food availability affect egg size: eggs laid later are larger, and this difference is significant (Ojanen et al., 1981; Jarvinen, Pryly 1989; Slagsvold, Lifjeld 1989; Magrath, 1992). Other researchers argue that larger eggs have been found in early clutches compared to late clutches. However, only length and volume differed significantly between early and late clutches (Mitrus et al., 2001).

Within the studied area, the length and diameter of early and late (eggs laid before the median date and after it) averaged over all years were L=17.98±0.76, d=13.35±0.46 and L=17.99±0.79, d=13.41±0.54 mm respectively, and did not differ significantly. Only in certain years, the differences in length, diameter, and volume are significant. In general, eggs from later clutches are larger, although in our case, in 2009 and 2018, length or diameter of eggs from later clutches were smaller. Late clutches from 2007, 2009, 2011, and 2017 stand out with high variability in length. Only in one case (2016) was high variability shown for the length of eggs in early clutches. High variability in egg length usually indicates instability in environmental conditions.

Weather conditions in 2016 were generally characterized by the late onset of meteorological summer (the average daily temperature exceeded +15°C on June 4th), as well as high average humidity in the decade pre-laying of the first egg (H=72.5 %). This is the highest humidity indicator recorded in the decade pre-laying of the first egg for the entire year of research.

The clutches of 2021 also characterized by high variability. The weather conditions this year were marked by a late onset of meteorological summer (June 4th, 2021). However, the humidity during the period preceding egg-laying was at the same level as in other years (H=56.0).

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Age and individual condition of female

The question of the influence of the female's age on the onset of the egg-laying period is a topic of debate (Perrins, 1970; Wiggins et al., 1994; Verhulst et al., 1995; Sanz, 1997). Some authors explain variations in egg sizes by the quality of the female or the territory (Ojanen et al., 1979; Potti, 1993; Nager, Zandt, 1994).

In short, egg size appears to be a characteristic of individual females, and yet the traits of a female that determine egg size are not clear. Although egg size often increases with female age (17 out of 37 studies), the change in egg size is generally less than 10%. Female mass and size rarely explain more than 20% of the variation in egg size within species. A female's egg size is not consistently related to other aspects of reproductive performance such as clutch size, laying date, or the pair's ability to rear young (Cristians, 2002).

There is also a hypothesis that the size of eggs is an inherited individual trait of the female (Mitrus at al., 2001).

The analysis of the materials from the collections of A. V. Nosachenko (Seliverstov, 2008) shows that some females have clutches with low variability in the length and diameter of the eggs, yet having individual characteristics in these parameters (all eggs are about 16.33×13.18; or about 19.44×13.82 mm). In our studies, such clutches have also been encountered (5-eggs clutch, L=18.9-19.2, CvL= 0.88). This suggests that there are individual traits in females carrying large or slow eggs regardless of clutch size and the date of the season.

The analysis of the repeatability of egg sizes in the same female did not provide a clear answer regarding the repeatability of diameter and length in the clutch of the same female two consequential years. There were cases found that both followed and did not follow this pattern.

C. Mitrus believes that egg size of the Collared Flycatcher from Białowieża Forest seems to depend more on the characteristics of the female than on environmental conditions (Mitrus et al., 2001). The diameter of the egg depends on the diameter of the female's oviduct and indicates, rather, her morphological conditions: it may indicate the presence of a significant portion of mature large females in the population. High variability suggests presence of different categories of females - both young and mature. Thus, in 2014-2018, there were eggs with a small diameter in the studied subpopulation. It should be assumed that this is related to the presence of young females.

Conclusion

In the studied subpopulation, the average egg length tends to decrease in the period from 2006 to 2021 and is slightly dependent on clutch size and the decade of first-egg laying.

Although, according to some authors (Mitrus et al.,2001), the age of the female has a negligible effect, and mainly the size of the egg depends on the size (weight and length of the legs) of the female. In our opinion, these indicators may demonstrate the maturity level of the female (but not age); thus, high oomorphological parameters over a series of long-term observations may indicate the share of reproductively most mature females in this subpopulation.

The diameter was the smallest in 2014-2015 and 2017-2018; then there was an increase in egg diameter to the usual size for this subpopulation. This may be related to the presence of young females in the subpopulation in 2014-2018.

In addition, it can be assumed that larger eggs are laid by females under optimal environmental conditions in the optimum of the range; as they move towards the borders of the range to the north and east, the morphometric parameters may decrease due to the decline in the quality (abundance of food) of the environment.

We suggest that among this subpopulation there is a significant proportion of mature females laying eggs of considerable size (which may explain the interannual differences in egg parameters).

Among the meteorological indicators we analyzed (temperature and humidity), the humidity of the pre-laying decade has a significant negative impact on the morphological parameters. The humidity during the egg-laying decade has a positive influence, while to a lesser extent, the temperature of the decade prior to egg-laying also positively affects the length of the eggs. The temperature of the previous decade and the number of rainy days play a minor role. At the same time, there is an optimum for these indicators (humidity 20 - 40 %), beyond which the effect of their influence on the size of the eggs changes to the opposite. In the studied area the length and diameter of eggs from early and late are did not differ significantly. Only in certain years, the differences in length, diameter, and volume are significant.

The analysis of the repeatability of egg sizes in the same female should answer the question of whether the size of the egg is an individual characteristics of the female. However, we did not receive a definitive answer. Cases were recorded both confirming and not confirming this. It may be related to the small number of repetitions (5 females, 2 years).

In the stable conditions of a national nature park, only the characteristics of the climate of the current year can provide variability in environmental conditions. The variability of oomorphological parameters is an integrated response to the instability of environmental parameters. One of the reasons for the high variability in egg sizes may be humidity. The size of the eggs itself cannot be explained by the 3climatic conditions of the current year. They are an integrated indicator of the female's maturity and the nutritional conditions of the season. These, in turn, are influenced by climatic features such as temperature, humidity, etc. High variability in egg length usually indicates instability in environmental conditions (in 2016 - hight humidity during the pre-lying period).

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Supplementary material

Table S1.

year	Clutch size	Clutches	Eggs	Lenght			diameter		
				M ± SD	lim	Cv (%)	M ± SD	lim	CV (%)
2006	3	1	3	18.27±0.25	18.0 - 18.5	1.38	13.30±0.26	13.1 - 13.6	1.99
	4	1	4	17.28±0.57	16.6-18.0	3.32	13.15±0.10	13.0-13.2	0.76
	5	4	20	18.50±0.58	17.20-19.20	3.16	13.57±0.48	12.5-14.3	3.52
	6	4	24	18.04±0.65	16.80-19.40	3.59	13.66±0.70	12.6-15.0	5.14
	7	2	14	17.68±0.46	16.7-18.6	2.63	13.43±0.24	13.1-13.9	1.79
	9	1	9	17.76±0.43	17.1-18.5	2.44	13.41±0.66	12.8-15.1	4.95
2007	5	1	5	19.04±0.22	18.7-19.3	1.15	13.7±0.14	13.5-13.9	1.03
	6	6	36	18.03±0.74	16.1-19.3	4.13	13.13±0.55	12.0-14.10	4.21
	7	18	126	17.94±0.64	16.5-20.1	3.56	13.40±0.39	12.1-14.2	2.89
	8	5	40	17.92±0.72	16.7-19.9	4.04	13.34±0.4	12.9-14.0	3
	9	2	18	18.31±1.06	17.0-20.20	5.76	13.66±0.21	13.4-14.0	1.55
2008	5	2	10	19.18±0.38	18.8-20.0	1.96	13.39±0.36	13.0-14.0	2.69
	6	4	24	18.47 ± 0.66	17.0-19.0	3.58	13.62±0.34	13.0-14.0	2.52
	7	13	91	18.04±0.58	16.5-19.0	3.2	13.31± 0.42	12.3-14.10	3.15
	8	11	88	18.08 ±0.66	16.6-19.10	3.64	13.2±0.42	12.1-14.2	3.15
	9	1	9	17.67±0.30	17.5-18.0	1.67	12.8±0.11	12.6-13.0	0.87
2009	5	1	5	18.42±0.40	18.0-19.0	2.15	13.02±0.08	12.9-13.1	0.64
	6	10	60	18.11±0.83	16.1-20.10	4.59	13.45±0.50	12.0-14.10	3.73
	7	15	105	18.28 ± 0.62	17.0-19.6	3.41	13.39±0.40	12.0-14.2	2.95
	8	5	40	17.59±0.50	16.6-18.9	2.86	13.68±0.41	12.9-14.0	2.99
	9	1	9	18.86±0.26	18.4- 19.2	1.36	13.57±0.18	13.4-13.9	1.33
2010	5	2	10	17.63± 0.64	17.00-18.90	3.64	13.01±0.09	12.90-13.10	0.67
	6	17	102	18.22±0.68	16.80-19.80	3.75	13.59±0.45	12.6-14.40	3.33
	7	22	154	18.11±0.73	16.3-20.00	4.03	13.44±0.47	12.00-14.10	3.48
	8	2	16	18.62±0.63	17.5-19.5	3.38	13.37±0.46	13.00-14.00	3.42
2011	4	1	4	16.4±0.52	15.9-16.9	3.19	12.78±0.52	12.0-13.1	4.06
	5	2	10	18.11±0.20	17.9-18.5	1.09	13.03±0.09	12.9-13.10	0.73
	6	6	36	18.61±0.63	17.50-20.0	3.39	13.92±0.27	13.50-14.70	1.91
	7	11	77	18.31±0.79	18.00-20.10	4.3	13.41±0.47	12.30-14.50	3.5
	8	11	88	17.93±0.79	15.9-19.00	4.39	13.32±0.43	12.3-14.0	3.2
2013	5	2	10	16.94±0.68	15.96-17.68	4.01	13.08±0.20	12.87-13.38	1.56
	6	2	12	18.37±0.4	17.61-18.84	2.2	13.40±0.4	12.55-14.07	2.98
	7	4	28	17.75±0.57	16.71-19.49	3.21	13.34±0.21	13.02-13.96	1.6
	8	4	32	17.91±0.8	16.8-19.1	4.45	13.42±0.4	12.69-14.1	3
2014	5	1	5	17.69±0.55	17.07-18.39	3.13	12.89±0.3	12.63-13.37	2.31
	6	5	30	17.93±0.44	16.50-18.70	2.44	13.06±0.30	12.20-13.79	2.28
	7	10	70	17.37±0.84	15.0-19.50	4.82	13.08±0.28	12.20-13.90	2.13
	8	2	16	17.81±0.56	16.2-18.34	4.32	13.00±0.20	12.53-13.19	1.55
	9	1	9	17.72± 0.57	17.00 - 19.00	0.32	13.04±0.14	12.8 - 13.30	1.09

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year	Clutch size	Clutches	Eggs	Lenght			diameter		
				M ± SD	lim	Cv (%)	M ± SD	lim	CV (%)
2015	4	3	12	17.9±0.53	17.13-18.88	2.97	13.24±0.29	12.89-13.95	2.19
	5	1	5	17.92±0.7	18.17-19.02	3.9	12.94±0.22	12.6-13.21	1.7
	6	5	30	17.65±0.65	16.12-18.9	3.65	12.94±0.62	11.15-14.07	4.78
	7	6	42	17.75±0.64	16.05-18.87	3.58	13.02±0.73	11.2-14.13	5.63
2016	4	1	4	17.32±0.62	16.6-17.99	3.55	13.15±0.37	13.0-13.87	2.74
	5	2	10	18.17±0.70	17.27-19.51	3.86	12.85±0.34	12.18-13.52	2.65
	6	5	30	18.14±0.89	16.61-19.92	4.93	13.33±0.52	12.01-14.10	3.89
	7	10	70	17.38±0.91	15.23-19.13	5.22	13.34±0.45	12.0-14.23	3.37
	8	1	8	17.7±0.36	17.16-18.15	2.02	13.43±0.13	13.28-13.66	0.94
2017	5	2	10	18.37±0.80	17.3-19.55	4.34	13.11±0.33	12.3-13.49	2.55
	6	7	42	17.59±0.73	16.46-19.53	4.14	13.11±0.47	12.12-14.53	3.6
	7	5	35	17.51±0.62	16.48-18.81	3.53	13.11±0.49	12.57-14.4	3.71
2018	6	3	18	17.51±0.48	16.07-18.03	2.75	12.87±0.20	12.4-13.3	1.53
	7	2	14	17.78±0.58	16.3-18.72	3.29	13.3±0.24	12.85-13.85	1.83
2019	4	2	8	17.91±0.67	17.09 - 18.73	3.74	13.63±0.13	13.45-13.76	0.97
	5	2	10	17.98±0.46	17.34 -18.7	2.54	13.51±0.26	12.92-13.82	1.91
	6	4	24	19.02±0.66	17.45 - 20.51	3.45	13.81±0.36	12.91-14.2	2.59
	7	1	7	17.51±0.78	16.58 - 18.75	4.47	13.46±0.25	12.93 - 13.82	1.83
	8	2	16	17.96 ± 0.44	17.35-18.99	2.44	13.53±0.39	12.86-14.64	2.85
2020	5	3	15	17.57± 0.73	16.89 - 19.08	4.15	13.57± 0.66	12.62-14.50	4.86
	6	6	36	17.71±0.47	16.56 - 18.53	2.65	13.42±0.52	12.55-14.02	3.9
	7	1	7	18.88±0.31	18.62- 19.42	1.63	13.23±0.36	12.53 - 13.57	2.68
2021	5	1	5	18.02±0.52	17.26 - 18.62	2.87	14.03±0.42	13.47-14.38	3.02
	6	6	36	17.99±0.66	16.66 - 19.05	3.67	13.69±0.47	12.43-14.8	3.4
	7	4	28	17.91±1.16	15.27 - 20.02	6.48	13.49±0.53	12.95-14.68	3.96

Table S2. Geographical and interannual variations in the length and diameter of the eggs of the Collared Flycatcher

	n (N)	L			d		
		min	max	M±m	min	max	M±m
Kharkivska gub (Somov, 1897)	(14)	16.5	17.8		12.0	13.2	
Uman`. Tal`noe (Cherkassy reg.. coll. Nosachenko) (Seliverstov, 2007)^				M±SD			M±SD
1922	3 (15)	17.5	19.5	18.21±0.57	13.0	13.5	13.33±0.16
1924	3(8)	16.1	19.6	18.76±1.19	12.4	14.1	13.58±0.58
1925	2(2)	17.5	18.9	18.2±0.99	12.9	13.4	13.15±0.35
1926	8 (23)	16.4	19.8	17.83±1.01	13.1	14.1	13.5±0.30
1927	1(4)	16.6	18.2	17.6±0.71	12.7	13.4	13.12±0.31
1928	9(28)	15.4	19.9	18.07±0.75	12.8	14.2	13.19±0.50
Kharkiv reg.Mochnach 21.05.1938 coll. Zubarovsky (Peklo,2018)	1 (6)	18.3	18.7		13.6	14.0	
Northern part of Ukraine (Marisova, Holina, 1959)	18 (78)	16.7	17.9	17.5±?	12.8	14.0	13.4±?
Kiev reg. Koncha-Zaspa. 23.05. 1978	1 (5)	18.3	18.7		13.1	13.6	
Ternopil` reg. (Talposch, Majhruk, 1995)	50 (249)	17.71	17.72		13.22	13.34	
Mitrus et al..(2001) - Białowieża Forest				Mean ± SD			Mean ± SD
1997	22	14.35	19.05	17.77±0.93	11.00	14.11	13.39±0.61
1998	33	16.40	19.30	17.8±0.84	12.80	14.02	13.34±0.30

	n (N)	L			d		
		min	max	M±m	min	max	M±m
1999	27	16.42	18.90	17.8±0.72	12.88	14.23	13.51±0.32
Sumy reg. N.P.Knysch (2003)				M±m			M±m
1990-1994	223 (1545)	16.2	19.8	17.96±0.09	12.4	13.3	13.31±0.04
1995-1998	14 (98)	15.9	20.4	17.82±0.07	12.4	14.0	13.25±0.04
1999	15 (103)	16.5	20.1	18.28±0.06	12.8	14.4	13.43±0.03
2000	19 (129)	16.5	19.8	17.92±0.05	12.5	14.6	13.35±0.03
2001	22 (147)	15.8	19.6	17.95±0.06	12.3	14.2	13.36±0.03
2002	21 (146)	16.7	19.5	18.20±0.03	12.3	14.1	13.34±0.03
Saval`sky lis (at 600 km to northern-east), 2003	51 (N=318)	15.5	21.0	M±m 17.73±0.07	11.5	15.4	M±m 13.24±0.03
West Europe (Makatsch,1976)	30	16.9	19.4	18.21	13.0	14.3	13.66

Table S3. Results of GAM models for egg dimensions, (a) – length, (b) – breadth, (c) – volume.
a) Formula:
L ~ SumFLD + s(SumFLD) + Sum30FLD + s(Sum30FLD) + Sum5 + s(Sum5) + Tprevdek + s(Tprevdek) + Tactdek + s(Tactdek) + MayIRain + s(MayIRain) + Fprevdek + s(Fprevdek) + Factdek + s(Factdek)

Parametric coefficients	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.0894249	0.1448537	-0.617	0.53708
SumFLD	-0.0053805	0.0072372	-0.743	0.45730
Sum30FLD	0.0007863	0.0100228	0.078	0.93748
Sum5	-0.0218133	0.0408415	-0.534	0.59334
Tprevdek	-1.0869296	0.4865653	-2.234	0.02561 *
Tactdek	-0.1211736	0.2189116	-0.554	0.57997
MayIRain	0.8497090	0.3853697	2.205	0.02758 *
Fprevdek	1.3626192	0.2744437	4.965	7.48e-07 ***
Factdek	-0.5985969	0.2066568	-2.897	0.00382 **

Approximate significance of smooth terms	edf	Ref.df	F	p-value
s(SumFLD)	7.1767	7.8363	3.687	0.000266 ***
s(Sum30FLD)	4.4579	5.6836	2.888	0.006505 **
s(Sum5)	0.1556	0.1556	2.451	0.536877
s(Tprevdek)	8.2126	8.2126	6.525	< 2e-16 ***
s(Tactdek)	7.3613	7.7439	3.673	0.000317 ***
s(MayIRain)	8.1513	8.1513	7.314	< 2e-16 ***
s(Fprevdek)	8.1100	8.1100	7.063	< 2e-16 ***
s(Factdek)	6.6628	7.3286	11.955	< 2e-16 ***

Significance codes: '***' – p<0.001, '**' – p<0.01, '*' – p<0.05
Rank: 73/81
R-sq.(adj) = 0.151 Deviance explained = 17.5%
GCV = 0.51195 Scale est. = 0.4969 n = 1974

(b) Formula:
d ~ SumFLD + s(SumFLD) + Sum30FLD + s(Sum30FLD) + Sum5 + s(Sum5) + Tprevdek + s(Tprevdek) + Tactdek + s(Tactdek) + MayIRain + s(MayIRain) + Fprevdek + s(Fprevdek) + Factdek + s(Factdek)

Parametric coefficients	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.248031	0.109378	2.268	0.023462 *
SumFLD	-0.013742	0.006593	-2.085	0.037243 *
Sum30FLD	0.013394	0.007133	1.878	0.060590
Sum5	0.185997	0.058502	3.179	0.001500 **
Tprevdek	0.597440	0.174205	3.430	0.000617 ***
Tactdek	-0.930216	0.219345	-4.241	2.33e-05 ***
MayIRain	-0.369461	0.308163	-1.199	0.230710
Fprevdek	1.334750	0.227516	5.867	5.23e-09 ***

Parametric coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Factdek	-1.025511	0.200856	-5.106	3.62e-07 ***

Approximate significance of smooth terms	edf	Ref.df	F	p-value
s(SumFLD)	8.032	8.114	3.107	0.019906 *
s(Sum30FLD)	1.745	2.503	3.982	0.022396 *
s(Sum5)	7.361	7.915	4.859	1.94e-05 ***
s(Tprevdek)	3.108	3.807	5.357	0.000742 ***
s(Tactdek)	8.199	8.199	5.384	5.83e-07 ***
s(MayIRain)	7.853	8.088	4.509	5.68e-05 ***
s(Fprevdek)	8.110	8.110	7.236	< 2e-16 ***
s(Factdek)	8.084	8.126	7.095	< 2e-16 ***

Significance codes: '***' – p<0.001, '**' – p<0.01, '*' – p<0.05
Rank: 73/81
R-sq.(adj) = 0.106 Deviance explained = 13.3%
GCV = 0.47722 Scale est. = 0.46266 n = 1974

(c) Formula:
V ~ SumFLD + s(SumFLD) + Sum30FLD + s(Sum30FLD) + Sum5 + s(Sum5) + Tprevdek + s(Tprevdek) + Tactdek + s(Tactdek) + MayIRain + s(MayIRain) + Fprevdek + s(Fprevdek) + Factdek + s(Factdek)

Parametric coefficients	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	134.2428	49.4673	2.714	0.00671 **
SumFLD	0.8205	2.3097	0.355	0.72243
Sum30FLD	9.4552	3.3003	2.865	0.00422 **
Sum5	51.3189	16.3660	3.136	0.00174 **
Tprevdek	-506.1788	172.7845	-2.930	0.00343 **
Tactdek	-66.2044	78.1550	-0.847	0.39705
MayIRain	80.8993	96.9504	0.834	0.40414
Fprevdek	545.0695	74.5418	7.312	3.85e-13 ***
Factdek	-445.5013	67.5481	-6.595	5.48e-11 ***

Approximate significance of smooth terms	edf	Ref.df	F	p-value
s(SumFLD)	7.871	8.073	3.142	0.001313 **
s(Sum30FLD)	3.207	4.317	5.159	0.000367 ***
s(Sum5)	6.324	7.257	2.942	0.020838 *
s(Tprevdek)	8.112	8.195	7.528	< 2e-16 ***
s(Tactdek)	8.199	8.199	6.595	< 2e-16 ***
s(MayIRain)	7.820	8.073	8.018	< 2e-16 ***
s(Fprevdek)	7.967	8.081	14.028	< 2e-16 ***
s(Factdek)	8.135	8.135	13.844	< 2e-16 ***

Significance codes: '***' – p<0.001, '**' – p<0.01, '*' – p<0.05
Rank: 73/81
R-sq.(adj) = 0.188 Deviance explained = 21.5%
GCV = 24428 Scale est. = 23619 n = 1974

Варіації розміру яєць у білошийої мухоловки (*Ficedula albicollis* Temminck, 1815)

Т. Атемасова, Т. Девятко, А. Атемасов

Метою цієї роботи було дослідити фактори, що впливають на варіацію розміру яєць білошийої мухоловки на південних межах поширення листяних лісів (Національний природний парк "Гомільшанські ліси", Україна). Загалом для аналізу були використані дані про 298 кладок і 1971 яйце білошийої мухоловки в штучних гніздівлях за період 2006–2011 та 2013–2021 років. Як метеорологічні показники використовувалася температура,

вологість та кількість днів з опадами. Всі статистичні аналізи були виконані із використанням програмного забезпечення R версії 4.4.2. Тест Шапіро–Уілка на нормальність виявив, що дані не розподілені нормально. Отже, для подальшого аналізу ми використовували тест Крусала – Уолліса та тест Данна, а також пермутаційний аналіз дисперсії (PERMANOVA) матриці відстаней. Для аналізу був використаний пакет vegan. Ми проаналізували вплив метеорологічних показників на розмір яєць, використовуючи узагальнені адитивні моделі. Статистичний аналіз проводився з використанням пакета mgcv.
У вивченій субпопуляції середня довжина яєць має тенденцію до зменшення в період з 2006 по 2021 рік і має слабку залежність від розміру кладки та декади відкладання першого яйця. Сезони з найменшими розмірами яєць у вивченій субпопуляції - 2014 - 2018 роки; після цього спостерігалось збільшення діаметра яєць до звичайного розміру для цієї субпопуляції. Можна припустити, що в цей період переважали молоді самиці.
Розміри яєць у досліджуваній субпопуляції і цілому подібні таким, що отримані в Сумській області України, і в певні роки перевищує показники яєць мухоловок з Біловезької пущі. Можна припустити, що більші яйця відкладають самиці у оптимумі ареалу; при наближенні до меж ареалу на північ і схід морфометричні параметри можуть зменшуватись.
Аналіз повторюваності розмірів яєць у однієї та тієї ж самки мав дати відповідь на питання - чи є розмір яйця індивідуальною характеристикою самки. Втім, ми не отримали остаточної відповіді.
Значний вплив на морфологічні параметри яєць має вологість декади, що передує початку відкладання яєць (негативний). Вологість під час декади несіння яєць має позитивний вплив на розміри яєць. Меншою мірою позитивно впливає температура декади, що передує несінню яєць, температура попередньої декади та кількість дощових днів. Водночас для цих показників існує оптимум (вологість попередньої декади 20-40 %), за межами якого вплив їх на розмір яєць змінюється на протилежний. На досліджуваній території довжина та діаметр яєць з ранніх і пізніх кладок не відрізнялися суттєво. Лише в окремі роки різниці в довжині, діаметрі та об’ємі були значущими.
Мінливість ooморфологічних параметрів є інтегрованою відповіддю на нестабільність екологічних умов. Однією з причин високої змінності розмірів яєць може бути вологість.

Ключові слова*: *Ficedula albicollis, розмір яйця, погодні умови

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