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Egg size variation in the Barn Swallow *Hirundo rustica*

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Abstract. Egg dimensions in 551 complete clutches (2469 eggs) of the Barn Swallow *Hirundo rustica* in the central part of Poland in 1979–1981 and 1994 were studied. Mean length ranged 19.4–19.7 mm, breadth 13.5–13.8 mm, and volume 1.8–1.9 cm^3. The length was not significantly different among years, but both the breadth and volume were. These mean egg dimensions were similar to those reported in a few other European studies, suggesting low geographic variation. Clutch mean egg lengths were weakly correlated with egg breadths. In some breeding seasons or parts of seasons egg size was significantly negatively correlated with the date of laying, hatching success and fledging success. Directions of some of these correlations were opposite to what was expected. No significant correlation was found between egg dimensions and clutch size or female/male wing lengths.

Key words: Barn Swallow *Hirundo rustica*, egg size, hatching success

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INTRODUCTION

Historically, variability of bird egg size was first studied as an illustration of the amount of variation available for natural selection (Bumpus 1896). Now egg size is considered as a component of fitness, since it positively influences the size of young birds at the moment of hatching and, consequently, their growth and survival (Schifferli 1973, Järvinen & Ylimaunu 1984, Galbraith 1988, Magrath 1992). However, clear evidence is scarce (review by Williams 1994). Life-history theory usually postulates that propagule size is a significant variable and thus is predicted to be involved in trade-offs with other variables, such as clutch size or timing of breeding (Roff 1992).

Egg size combined with clutch size constitutes a major energetic investment of females and so it could be expected that these two variables should be negatively correlated. It is also conceivable that egg size is constrained by the body size and/or age of females, which would result in a positive correlation between egg size and female body size. Such a relation has indeed been reported for some species (e.g. Ojanen *et al.* 1978, Svensson 1978, Otto 1979, Grant 1982, Potti 1993). Scarce comparative data on the Barn Swallow egg size variation are available (Nitecki 1964, Kuźniak 1967, Pikula & Beklova 1987, Brichetti 1992). Ward (1995) has provided data concerning Barn Swallow egg size variation in relation to several potential explaining variables. In another paper (Bańbura & Zieliński 1995) we have demonstrated that no clear pattern of laying-sequence-related variation of egg dimensions within clutches exists in this species. No influence of ambient temperature on egg size has either been recorded.

Here we present a general description of egg size variability in a Polish population of the Barn Swallow. We focus on the interclutch and interfemale variation. We also try to find a link between egg size and some other life history traits and breeding characteristics.

MATERIAL AND METHODS

Egg characteristics were recorded for this study at small farms located in the Łódź province in central Poland near the village of Ktery (52°15'N, 19°25'E) from June 1979 to September 1981 and at Goślub (52°05'N, 19°28'E) from May to September 1994. Most clutches studied in 1979–1981 were late clutches (repeat or second and, occasionally, third clutches). In 1994 we studied both first (early clutches) and late clutches. We measured 2469 eggs from 101, 211, 187 and 52 full clutches in 1979, 1980, 1981 and 1994, respectively.

We measured the length (L) and breadth (B) of eggs to the nearest 0.1 mm with a sliding calliper and calculated the volume using the formula:

$$V = 0.507LB^2$$

which was worked out by Manning (1979) for the American subspecies of the Barn Swallow. Mean values of egg dimensions for full clutches were used as observational units in this paper.

The histories of particular nests were followed as strictly as possible. When laying was not observed, we estimated the date of first egg laying using data on nestling wing growth rate (Zieliński 1993), assuming that one egg is laid every day and that incubation lasts 14 days after laying the final egg (our data). Hatching success was estimated as the percent of hatched eggs in the full clutch and fledging success as the percent of full clutch eggs that gave fledglings.

Adult birds were captured in mist nets at nesting sites and their wing length was measured to the nearest 0.1 mm. The procedure applied was described by Bańbura (1986).

Mean monthly temperatures and mean sum of rainfall for the breeding seasons 1979–1981 were: May — 13.03°C, 30.87 mm; June — 17.13°C, 89.9 mm; July — 16.19°C, 101.57 mm; August — 16.5°C, 51.2 mm and in 1994 mean monthly temperatures and sum of rainfall were: May — 14.1°C, 72.2 mm; June — 17.7°C, 17.6 mm; July — 24.1°C, 43.2 mm and August — 19.7°C, 26.6 mm. The data were obtained from meteorological stations Błonie (1979–1981) and Borów (1994) located near the study sites.

Statistical procedures were used after Sokal & Rohlf (1981) and Zar (1984).

RESULTS

General characteristics of variation in egg length, breadth and volume (Tab. 1 and Tab. 2) were based on clutch means. The data for 1994 were analysed for differentiation between the first and late (second and repeat) broods (Tab. 2). There was no significant difference between these categories of broods. As in 1979–1981 only late clutches were available for the analysis, we used the same category of the 1994 clutches for the interyear comparison of egg dimensions.

Table 1. Means, standard deviations (SD) and coefficients of variation (CV) of egg length (L — mm), breadth (B — mm) and volume (V — cm^3), n = the number of clutches. ANOVA for differences among means including the late clutches of 1994.

[Tabela 1. Średnie arytmetyczne, odchylenia standardowe (SD) i współczynniki zmienności (CV): długości (L — mm), szerokości (B — mm) i objętości (V — cm^3) jaj, n = liczba lęgów. Analiza wariancji dla różnicy między średnimi z uwzględnieniem późnych lęgów z roku 1994.]

Year		Mean	SD	CV	n
1979	L	19.55	0.798	4.08	101
	B	13.62	0.369	2.71	101
	V	1.841	0.127	6.91	101
1980	L	19.63	0.841	4.28	211
	B	13.81	0.403	2.92	211
	V	1.9	0.148	7.78	211
1981	L	19.71	0.804	4.08	187
	B	13.72	0.386	2.81	187
	V	1.884	0.138	7.32	187
ANOVA	L	F = 1.798; df: 3.523; p > 0.2			
	B	F = 5.392; df: 3.523; p < 0.005			
	V	F = 3.934; df: 3.523; p < 0.02			

There was no significant interyear difference found among mean lengths of eggs. Mean egg breadths and volumes for late clutches proved significantly different among years (Tab. 1), which was due to differences between the years 1979 and 1980. Tukey's test was applied in both cases: $q = 5.47$, $p < 0.01$ for breadth and $q = 4.83$, $p < 0.01$ for volume, df = 4.523. No other interyear difference was significant.

Covariation of egg length and breadth as measured by correlation between clutch mean length and width was very weak (Tab. 3). This was only significant in 1980.

In no year the egg traits analysed were significantly correlated with either the mother or father wing length. No correlation with clutch size was demonstrated either. A few casewise significant correlations appeared

Table 2. Means, standard deviation (SD) and coefficients of variation (CV) of egg length (L — mm), breadth (B — mm) and volume (V — cm³) in the first and late (second and repeat) clutches in 1994. The t-tests for differences between the egg traits in the clutch categories.

[Tabela 2. Średnie arytmetyczne, odchylenia standardowe (SD) i współczynniki zmienności (CV): długości (L — mm), szerokości (B — mm) i objętości (V — cm³) jaj dymówki w pierwszych i późnych (drugich i powtarzanych) lęgach w roku 1994. Test *t* dla różnic między średnimi wartościami badanych cech.]

Clutches		Mean	SD	CV	n
First	L	19.36	0.734	3.79	24
	B	13.83	0.489	3.54	24
	V	1.881	0.171	9.09	24
Late	L	19.39	0.631	3.25	28
	B	13.80	0.515	3.73	28
	V	1.875	0.162	8.64	28
Pooled	L	19.38	0.674	3.48	52
	B	13.81	0.499	3.61	52
	V	1.877	0.164	8.74	52
t-test	L	t = 0.122; df = 50, ns			
	B	t = 0.200; df = 50, ns			
	V	t = 0.132; df = 50, ns			

between egg dimensions and the onset of clutch laying, hatching success and fledging success (Tab. 4). Egg length was positively correlated with the laying date in 1979 (late clutches). In the first brood of 1994 both egg breadth and volume were negatively correlated with the time of laying. All significant correlations of egg traits with hatching or fledging success were negative (Tab. 4). However, these results should be interpreted with caution because accepting the 5% significance level, 5 correlations out of 100 can be significant by chance (Rice 1989).

DISCUSSION

Overall, mean values and variation in egg dimensions in this study are close to those reported for another Polish population (Nitecki 1964), for Czechoslovak materials described by Pikula & Beklova (1987), for Scotland (Ward 1995) and for Italy (Brichetti 1992). Since they are also very similar to averages recorded by Cramp (1988) it seems reasonable to suppose that there is low geographic variation of these traits in Europe, though further studies should be undertaken to obtain a definite answer.

The weak correlation between egg length and breadth reported in this study seems typical of many bird species (e.g. Van Noordwijk *et al.* 1981, Ojanen

Table 3. Correlations (r) between clutch mean egg breadths and lengths during the course of this study. Degrees of freedom (df) result from the number of clutches.

[Tabela 3. Korelacja średniej lęgowej szerokości i długości jaj w poszczególnych latach badań. Liczby stopni swobody (df) wynikają z liczby lęgów.]

	1979	1980	1981	1994 First	1994 Late	1994 Pooled
r	0.038	0.174	0.128	0.300	0.214	0.253
df	99	209	185	22	26	50
	p > 0.5	p < 0.02	p > 0.05	p > 0.1	p > 0.2	p > 0.1

Table 4. Correlations between the length (L), breadth (B) and volume (V) of eggs and the onset of laying, hatching success and fledging success. * p < 0.05; ** p < 0.01; 1994 f — first clutches, 1994 l — late clutches.

[Tabela 4. Współczynniki korelacji między długością (L), szerokością (B) a objętością (V) jaj a datą rozpoczęcia lęgu, sukcesem klucia i sukcesem wylotu. 1994 f — pierwsze lęgi, 1994 l — lęgi późne.]

		Laying date	Hatching success	Fledging success
1979	L	0.245*	–0.258*	–0.046
	B	–0.109	0.043	0.113
	V	0.060	–0.126	0.056
	n	85	68	40
1980	L	–0.041	0.017	0.066
	B	0.130	–0.019	0.038
	V	0.080	–0.009	0.064
	n	177	155	89
1981	L	0.010	–0.037	–0.090
	B	0.020	0.112	0.080
	V	0.008	0.065	0.009
	n	178	164	88
1994 f	L	–0.250	–0.335	–0.459
	B	–0.507*	–0.171	–0.534*
	V	–0.509*	–0.266	–0.627**
	n	24	20	17
1994 l	L	–0.105	–0.530*	–0.440
	B	–0.262	–0.023	–0.260
	V	–0.265	–0.193	–0.356
	n	28	17	14
1994 f+l	L	–0.089	–0.333*	–0.427*
	B	–0.247	–0.097	–0.466*
	V	–0.243	–0.211	–0.550*
	n	52	37	31

1983, Jarvinen & Pryl 1989, Potti 1993). This relation is very often studied, but usually with single eggs as sampling units. Such a procedure is incorrect because eggs in a clutch are not independent (Jarvinen & Pryl 1989). Pikula & Beklova (1987) reported a significant correlation between egg length and breadth of the Swallow using the single egg approach.

Significant correlation between egg dimensions and female body size was revealed in a number of studies, the relation being usually stronger with female weight than with wing length (e.g. Ojanen *et al.* 1979, Järvinen & Väisänen 1983, Järvinen & Pryl 1989, Potti 1993, Nager & Zandt 1994, Horak *et al.* 1995). Although a certain level of such correlation is expected to result from both proximate and ultimate factors (Ojanen 1983, Perrins 1996), it is weak, as a rule.

For most temperate bird species the timing of breeding is a very important aspect of their life-histories; this results in a decline of clutch size and other breeding parameters with the progress of the breeding season (Lack 1950, Perrins 1970). Accordingly, negative relations between egg size and laying date were described in studies on a variety of species (Parsons 1972, Murton *et al.* 1974, Furness 1983; Byrkjedal & Kalas 1985, Soler 1988, Heeb 1994). This is also true of the Barn Swallows analysed here in 1994. On the other hand, there is no clear explanation for the positive relation observed in 1979. Anyway, it seems probable that the correlation between egg size and time of laying in the first brood is independent of that in the late broods.

Life-history theory suggests that egg size should be negatively traded-off with clutch size (Smith & Fretwell 1974, Roff 1992). This should result in a negative genetic correlation, which, however, can be obscured when phenotypic correlations are analysed. The negative correlation has been observed in comparative studies at the interspecific level (Lack 1968, Rohwer 1988, Blackburn 1991). Similarly to some other studies (Järvinen & Pryl 1989, Potti 1993, Heeb 1994, see also Ojanen *et al.* 1978 and Horak *et al.* 1995), no correlation of egg dimensions with clutch size was found in this study. However, a lack of this phenotypic correlation does not disprove the existence of a life-history trade-off between clutch size and egg size because even a high genetic correlation can be completely reversed at the phenotypic level (Reznick 1985). Järvinen (1996) has recently studied the trade-off between egg size and clutch size in Pied Flycatchers *Ficedula hypoleuca* in cold and warm summers and shown that such a trade-off has been more apparent in cold seasons. He has concluded that the trade-off may be obscured in central parts of species areas where climate is usually warmer.

The negative correlation between egg size and hatching and fledging success observed in some cases in the present study is an unexpected result. Usually positive effects have been observed, with small eggs being characterised by low hatchability (Ojanen 1983, Potti & Merino 1996). One possible explanation for the modification of an expected positive influence of egg size on nestling survival (Williams 1994) is that egg size affects a structural size component of body mass rather than a "condition" component (Magrath 1992). It is the latter which eventually determines juvenile survival.

Considerable egg size variation observed in many avian populations may result from selection pressures fluctuating over years. It is almost certain that there is no single optimal egg size but rather there is a range of more or less equivalent egg sizes considered as just one aspect of reproductive tactics (Nur 1986). This tentative suggestion seems to find support in Järvinen's (1996) results on Flycatcher egg sizes in extreme, climatically variable environments.

Generally, it seems evident that the processes causing particular interrelations between egg dimensions and other life-history variables in relation to environmental variables are very complicated. Some subtle relations may be masked by environmental effects (e.g. Järvinen 1996). Experimental approach is evidently needed to account for some of this complexity (Magrath 1992, Nilsson & Svensson 1993, Smith *et al.* 1995, Foger & Pegeraro 1996). The experiments which have already been conducted have supported some interesting although mutually inconsistent results.

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STRESZCZENIE

[Zmienność rozmiarów jaj dymówki]

Materiał do badań zbierano w latach 1978–1981 w Polsce środkowej w gospodarstwach rolnych położonych we wsi Ktery i okolicach oraz w roku 1994 w gospodarstwie hodowlanym Goslub. Obszar badań położony był w sąsiedztwie rzeki Bzury. Wszystkie gniazda były numerowane i systematycznie kontrolowane tak, że możliwe było śledzenie historii gniazd aż do momentu zakończenia lęgu. W szczególności ustalano datę rozpoczęcia składania jaj, wielkość zniesienia, liczbę piskląt wyklutych z jaj i liczbę piskląt wylatujących z gniazda. Za pomocą sieci typu mist-net odławiano dorosłe ptaki przebywające w gniazdach lub w ich pobliżu. Ptaki dorosłe były chwytane, mierzone i uwalniane (patrz Banbura 1986). Długość (L) i szerokość (B) jaj mierzono przy pomocy suwmiarki z dokładnością do 0,1 mm. Objętość obliczano według wzoru: $V = 0{,}507\ LB^2$, który został opracowany przez Manninga (1979) dla amerykańskiego podgatunku dymówki *Hirundo rustica erythrogaster*. Do analizy wykorzystano tylko lęgi pełne, tj. takie, w których nie przybywało już jaj i które były wysiadywane przez samicę. Ogólna charakterystyka rozmiarów jaj została przeprowadzona na podstawie średnich lęgowych a nie cech pojedynczych jaj, co pozwala uniknąć obciążenia statystycznego wynikającego z braku niezależności cech jaj wchodzących w skład danego lęgu.

Nie stwierdzono istotnych statystycznie różnic między latami w długości jaj. Natomiast dla lęgów późnych zarówno dla szerokości jak i objętości jaj różnice między latami okazały się istotne statystycznie (tab. 1 i 2). Średnie lęgowe długości jaj były słabo skorelowane z szerokością (tab. 3). W żadnym z lat badane cechy jaj nie były istotnie skorelowane z długością skrzydła samca czy też samicy. Odnotowano kilka istotnych statystycznie korelacji między rozmiarami jaja a datą rozpoczęcia lęgu, sukcesem klucia i sukcesem wylotu. Długość jaj z późnych lęgów z 1979 roku była dodatnio skorelowana z datą rozpoczęcia lęgu. Natomiast w pierwszych lęgach z 1994 roku szerokość i objętość jaj były ujemnie skorelowane z datą rozpoczęcia lęgu. Wszystkie istotne korelacje między wielkością jaja a sukcesem klucia i sukcesem wylotu były ujemne (tab. 4). Średnie rozmiary jaj były podobne do podawanych z innych rejonów Europy, co wskazuje na stosunkowo niewielką geograficzną zmienność rozmiarów jaj dymówki.

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