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The effect of egg size on hatching rate in the Tree Sparrow *Passer montanus* (study in Central Poland)

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Abstract. The analysis covered 1332 Tree Sparrow eggs, 1053 of them hatched, in 257 clutches of which 114 were fully successful, 119 partially so, and 24 were deserted. The mean egg mass in deserted clutches was lower than in clutches where hatching success was total or partial but not significantly so. The mean hatching success per clutch increased with the mean egg mass. The individual eggs in fully hatched clutches weighed significantly more (2.21 g) than those in partially hatched clutches (2.17 g), and were also heavier than "infertile" eggs (2.14 g). During nest inspections to ascertain the egg laying sequence, the egg mass in 5-egg clutches with full and partial hatching success was found to be higher than in deserted clutches. The eggs in fully hatched clutches were broader than "infertile" eggs.

Key words: egg size, hatching rate, Tree Sparrow, *Passer montanus*

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INTRODUCTION

Many authors have shown that egg size (mass) affects hatching rate. Larger eggs produce a higher percentage of nestlings, or the mass of hatched eggs is higher than that of unhatched eggs (Dawson 1972, Koivunen et al. 1975, Bolotnikov et al. 1978, 1985, Järvinen & Väisänen 1983, Ojanen 1983a, Perrins 1996, Potti & Merino 1996, Weidinger 1996, and others). However, many other authors have not found such a relationship (Schifferli 1973, Koenig 1982, Briskie & Saale 1990, Smith et al. 1995, Ward 1995, and others). Larger eggs produce larger nestlings (Schifferli 1973, Bryant 1978, Blomquist, Johansson & Götmark 1997, and others). This could provide a selection force in favour of large eggs. On the other hand, selection for small eggs might result from benefits for the female investing less energy in egg formation (Van Noordwijk et al. 1981).

Does egg mass influence the hatching rate, and has it fitness consequences? Answer to these questions is the subject of this study with regard to Tree Sparrow (*Passer montanus*) eggs.

STUDY AREA, METHODS AND MATERIAL

The study was carried out in the villages of Dziekanów Leśny, Dziekanów Polski, and Kiełpin, situated between the Vistula river and the Kampinos National Park, about 15 km NW of Warsaw (52°20′N, 20°50′E), where 200 nest-boxes were erected. As no differences were found in egg size among these villages (Pinowski et al. 2001), all the data were pooled and analysed jointly. The material was collected in 1994 (15 April–20 August) and in 1995 (20 April–20 July). During the laying period, nest-boxes were inspected daily between 09.00 and 14.00. Eggs were marked with a permanent marker on the day of laying, so we knew the laying sequence. The egg length (L) and maximum breadth (B) were measured to the nearest 0.1 mm, using vernier callipers in both study years. In 1995, eggs were also weighed on the day of laying to the nearest 0.01 g using an electronic balance. Assuming that the intercept equals to zero, the regression of egg mass (M) on the product $L \times B^2$, approximately proportional to egg volume, was calculated:

$$M = 0.000546 \times L \times B^2 \ (r = 0.90, p < 0.001).$$

where M is in grams, L and B in millimetres.

To analyse the data from both years jointly, all references to Tree Sparrow "egg-mass" in this paper indicate the egg mass predicted from this equation and not the weighed fresh-egg mass. To know from which egg a nestling hatched, nest-boxes were visited during hatching. The clutches were categorised into successful and unsuccessful. Among successful clutches we distinguished: fully successful clutches in which all eggs hatched, and partially successful clutches in which only some eggs hatched. Unsuccessful clutches were grouped into deserted and totally destroyed (by predators, humans, or as a result of nest-box fall). In total, 257 clutches were analysed (Table 1). Eggs from clutches where no one nestling hatched were excluded from the analysis of individual eggs, except for deserted clutches (Table 2). The unhatched eggs from partially successful clutches were assigned to three groups: eggs disappeared during incubation, eggs destroyed by observers, which were eliminated from later analysis, and eggs that remained unhatched in the nest after hatching of the other eggs.

Table 1. Number of clutches (N) analysed in successive broods (I, II, III). %fs — clutches with full hatching success, %ps — clutches with partial hatching success, %d — deserted clutches

Brood	N	% fs	%ps	% d
1994				
I	65	41.5	52.3	6.2
II	35	37.1	57.1	5.7
III	19	47.4	47.4	5.3
1995				
I	58	44.8	36.2	19.0
II	46	56.5	37.0	6.5
III	34	38.2	52.9	8.8
Total	257	44.4	46.3	9.3

The eggs from which no nestlings hatched were later broken open to check whether they contained a dead embryo. If no embryo was found there, then they were described as "infertile" (I). This group could contain also the eggs which were in fact fertile but the embryo died at such an early stage of development, that it was impossible to recognize it (Pinowski 1968, Birkhead et al. 1995). In the study of Birkhead et al. (1995) on the House Sparrow, among "infertile" eggs only 27 % were truly infertile and 73 % failed to hatch because of early embryo mortality. Other unhatched eggs were with visible dead embryos (D) and with embryos that died during hatching (D/H). In total, 1332 eggs were analysed (Table 2).

Egg mass differed among clutches, and the mass of individual eggs in a clutch was related to their laying sequence (Pinowski et al. 2001). To eliminate these two sources of variation, a mean mass of successive eggs in fully successful

Table 2.Number of eggs (N) analysed in successive broods. Categories of unhatched eggs: I — infertile or without visible embryo, D — dead embryo, D/H — dead during hatching, disap. — disappeared during incubation, destr. — destroyed during nest control, desert — eggs from deserted clutches.

Brood	N	Hatched	unhatched		I	D	D/H	disap.	destr.	desert
		N	N	%	%	%	%	%	%	%
1994										
I	357	288	69	19.3	34.8	18.8	11.6	2.9	2.9	29.0
II	187	145	42	22.5	28.6	23.8	9.5	9.5	14.3	14.3
III	94	77	17	18.1	41.2	11.8	11.8	0.0	5.9	29.4
1995										
I	290	215	75	25.9	17.3	5.3	9.3	10.7	5.3	52.0
II	237	199	38	16.0	26.3	21.1	5.3	2.6	10.5	34.2
III	167	129	38	22.8	36.8	23.7	2.6	2.6	13.2	21.1
Total	1332	1053	279	20.9	28.7	16.5	8.6	5.7	7.9	32.6

clutches and with known laying sequence was calculated for 437 eggs of 4-, 5-, and 6-egg clutches separately. Then the ratio of the mean mass of eggs laid as the first, the second, etc. to the mean mass of all eggs from clutches of a given size was calculated and expressed as percentage. In this way, a pattern of changes in egg mass in relation to laying sequence was obtained for 4-, 5-, and 6-egg clutches. Based on this pattern, mass m_w of each egg from 4-, 5-,and 6-egg clutches with known laying sequence was calculated from the formula:

$$m_w = \frac{p_{k,n}}{100} m_{mean}$$

where $p_{k,n}$ is the ratio of mean mass of egg k from n-egg clutch to the mean mass of all eggs in n-egg clutches, and m_{mean} is the mean egg mass from the clutch in which this egg was laid. The difference was calculated between the mass of a given egg and the mass calculated from the pattern to see which egg categories deviated from the pattern.

An analysis of variance and limit significant difference (LSD) test were used to estimate differences in the mean egg mass, mean of the mean mass of an egg in the clutch, and mean deviation of an egg mass from its calculated value. Log-transformed deviations of egg mass from the pattern were used for statistical comparisons. Proportions of various clutch and egg categories were compared by using chi-square test.

RESULTS

Mean egg mass in a clutch and hatching rate

In total, 257 clutches were analysed in the two study years jointly, including 114 fully successful, i.e. with all eggs hatched, 119 partially successful, and 24 abandoned clutches. The most frequent cause of clutch loss was desertion by parents (Table 1) and destruction of whole clutches (1.2 %).

In all broods, the percentage of fully successful, partially successful, and deserted clutches was similar ($\chi^2 = 13.95$, df = 10, $p > 0.17$; Table 1).

Significant differences were in clutch size among fully successful, partially successful, and deserted nests ($\chi^2 = 87.17$, df = 12, $p < 0.001$) due to a higher proportion of small clutches in the group of deserted nests (Fig. 1), presumably deserted before clutch completion. By subtracting from the total number of deserted clutches the minimum number of deserted smallest clutches, so that the frequency distribution of the deserted clutches was not significantly different from the frequency distribution of the fully successful and partially successful clutches, it was calculated that at least 41.7% (10 of 24) of the deserted clutches were not complete, that is, deserted during egg laying.

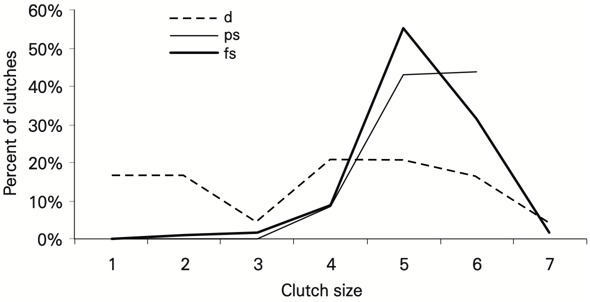

Fig. 1. Distribution of clutch sizes for clutches with full hatching success (fs), partial hatching success (ps), and deserted clutches (d).

The mean mass of an egg in the clutch did not differ significantly among clutch categories (ANOVA: F = 0.964, $p > 0.38$), although mean values of the mean mass of an egg in the clutch were a little higher for the groups of fully successful clutches (2.21 ± 0.16, n = 114) and partially successful clutches (2.22 ± 0.15, n = 119) than for deserted clutches (2.18 ± 0.23, n = 24). For the group of 4-6-egg clutches (n = 236), an increase in the mean mass of an egg in the clutch was significantly related to an increase in the number of more successful clutches (Fig. 2).

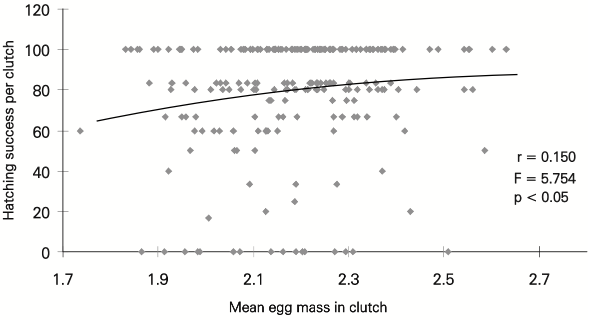

Fig. 2. Multiple regression of hatching success on mean egg mass for 4-, 5-, and 6-egg clutches.

Mass of individual egg in clutch and hatchability

In both study years, 1332 Tree Sparrow eggs were analysed, including 1053 hatched eggs. The most often causes of hatching failure in partially

Table 3. Mean masses (g), lengths (mm), breadths (mm) and shape indexes (%) of different egg categories in clutches with full hatching success, partial hatching success, and deserted. Egg categories (I, D and D/H) as in Table 2. a, b — results of LSD test for mass. A, B — result of LSD test for breadth. Two means are significantly different ($p < 0.05$) if they are not denoted by the same letter. Series of means without letters are not significantly different

Egg category	Clutch category	
	full success mean ± SD	partial success mean ± SD
Hatched		
Mass	2.21a ± 0.19	2.17^{b} ± 0.18
Length	19.46 ± 0.95	19.35 ± 0.90
Breadth	14.40^{A} ± 0.44	14.34^{AB} ± 0.45
shape index	74.10 ± 3.77	74.25 ± 3.61
	n = 593	n = 460
I (n = 80)		
Mass		2.14^{b} ± 0.23
Length		19.29 ± 1.00
Breadth		14.24^{B} ± 0.54
Shape index		73.97 ± 3.84
D (n = 46)		
Mass		2.19^{ab} ± 0.21
Length		19.47 ± 0.91
Breadth		14.33^{AB} ± 0.52
Shape index		73.71 ± 3.69
D/H (n = 24)		
Mass		2.18^{ab} ± 0.21
Length		19.55 ± 0.91
Breadth		14.27^{AB} ± 0.48
Shape index		73.09 ± 3.12
Desert (n = 91)		Deserted clutches
Mass		2.18^{ab} ± 0.23
Length		19.23 ± 0.12
Breadth		14.38^{B} ± 0.50
Shape index		74.98 ± 4.16

successful clutches in the sequence of importance were "infertile" eggs, death of embryo, death of nestling during hatching, and egg disappearance during incubation (Table 2).

It has been found for 1294 eggs (excluding eggs that disappeared and destroyed eggs) that the mean mass of eggs in fully successful clutches was significantly higher than the mean mass of hatched eggs from partially successful clutches and "infertile" eggs (ANOVA: $F = 2.318$, $p < 0.05$; Table 3).

The mean mass of eggs in 4-, 5-, and 6-egg clutches with full hatching success increased from the first to penultimate egg, and was a little lower for the last egg (Fig. 3).

A significant difference in the mean egg mass among fully successful, partially successful and deserted clutches was found only for 5-egg clutches (two-way ANOVA: $F = 8.08$, $p < 0.001$; Fig. 3B).

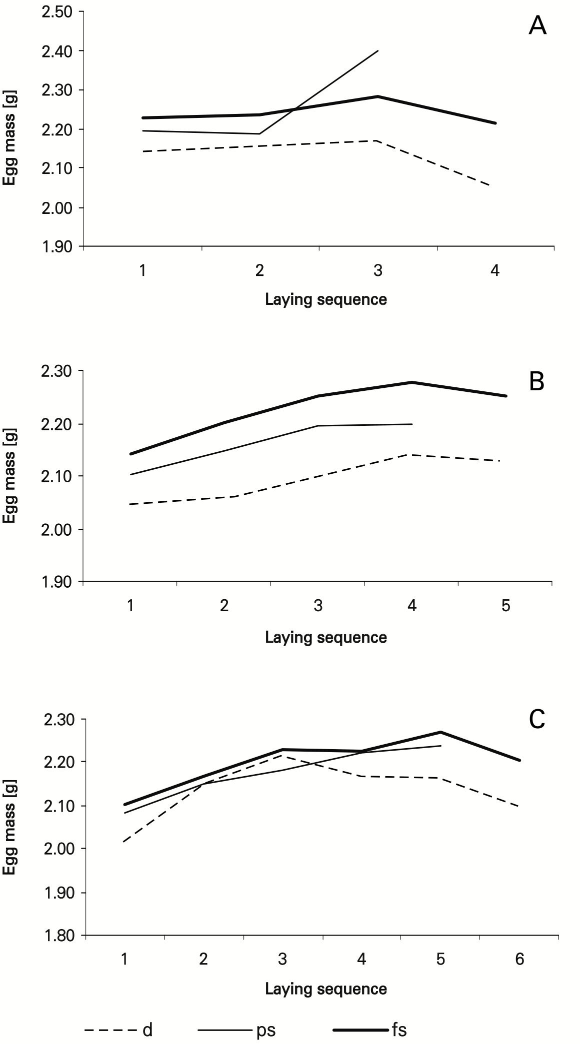

Fig. 3. Mean mass of successive eggs in 4- (A), 5- (B), and 6-egg (C) clutches for clutches with full hatching success (fs), partial hatching success (ps) and deserted ones (d). In A $n_{fs} = 28$, $n_{ps} = 30$, $n_{d} = 12$; in B $n_{fs} = 244$, $n_{ps} = 198$, $n_{d} = 15$; in C $n_{fs} = 165$, $n_{ps} = 253$, $n_{d} = 24$.

No differences were found in the proportion of hatched and unhatched eggs (I, D, and D/H) in relation to laying sequence (chi-square test: $\chi^2 = 9.110$, df = 6, $p > 0.16$ for 4-egg clutches; $\chi^2 = 10.316$, df = 8, $p > 0.16$ for 5-egg clutches; $\chi^2 = 10.877$, df = 10, $p > 0.36$ for 6-egg clutches).

In fully successful clutches, the mass of eggs 1, 2, etc. accounted for 95.3% to 102.7% of the mean mass of all eggs from a given clutch size (Table 4). For eggs from clutches with full hatching success, the mean deviation of an egg mass from the value calculated from the pattern was 0.04 g, and it was significantly lower than for eggs from clutches with partial hatching success, "infertile" eggs, and for eggs from deserted clutches (Table 5).

Table 4. Pattern of changes in mean mass of an egg in a clutch.

Laying sequence	Clutch size 4 %	5 %	6 %
1	99.5	96.2	95.3
2	99.8	98.7	98.3
3	101.8	101.0	101.1
4	98.8	102.2	100.9
5		101.1	102.7
6			99.9

Table 5. Deviation of the mean mass of an egg (g) from the mass calculated from the pattern for different egg categories, as in Table 2. "a" and "b" — results of LSD test. Two means are significantly different ($p < 0.05$) if they are not denoted by the same letter.

	Clutch category	
Egg category	full success geo-mean min — max	partial success geo-mean min — max
Hatched	0.04^{a} 0.00 — 0.69 n = 423	0.06^{b} 0.00 — 0.36 n = 335
I n = 60		0.06^{b} 0.00 — 0.503
D n = 30		0.05^{ab} 0.00 — 0.24
D/H n = 19		0.09^{ab} 0.02 — 0.34
		deserted clutches
desert n = 50		0.07^{b} 0.01 — 0.33

No significant differences were found in egg length among egg categories (ANOVA: F = 1.87, p > 0.09), but some differences in egg breadth were significant (ANOVA: F = 2.233, $p < 0.05$): between eggs from fully successful clutches and eggs from deserted clutches, and also between eggs from fully successful clutches and "infertile" eggs (Table 3). Shape index was similar in all egg categories (ANOVA: F = 1.518, p > 0.18; Table 3).

DISCUSSION

In this study we found that the mean mass of an egg from deserted clutches was magnificanly lower than that from clutches with full and partial hatching success. In the group of 4–6-egg clutches, an increase in the mean mass of an egg in the clutch corresponded to an increase in the number of clutches with higher hatching success (Fig. 2). Analysing the mass of individual eggs, we found that the mass of an egg from clutches with full hatching success was higher than the mass of an egg from clutches with partial hatching success (Table 3). A similar relationship was found by O'Connor (1979), Järvinen & Väisänen 1983, Potti & Merino (1996) for various bird species. In the Tree Sparrow, deserted eggs were lighter than eggs from fully successful clutches, as also found in the Great Tit (Dufva 1996). In the Collared Flycatcher *Ficedula albicollis*, deserted eggs were laid by lighter females (Wiggins et al. 1994). This implies that eggs in deserted clutches were laid by females in poorer condition. The mass of "infertile" eggs of Tree Sparrows was lower than that of fertile eggs, that is, from clutches with full hatching success (Table 3). Also Dawson (1962) found that "infertile" eggs and eggs with dead embryos had lower mass than the eggs that hatched. Nilsson & Svensson (1993) found that clutches of Blue Tit *Parus caeruleus* with a low average egg mass tended to contain more unhatched eggs, however, no signs of reduced hatchability of small eggs within a clutch were detected. Magrath (1992) showed that egg mass of Blackbird *Turdus merula* had little effect on hatching success, except for very light "runt" eggs which made up less than 1% of the eggs laid. Zieliński & Bańbura (1998) found even negative correlations between egg length and hatching success in Barn Swallow *Hirundo rustica*. They explain this after Nur (1986) that there is no single optimal egg size but rather a range of more or less equivalent egg sizes considered as just one aspect of reproductive tactics.

The failure of an egg to hatch may result from infertility, from genetically determined developmental defects, from improper exchange rates of respiratory gases and water vapour, from failures of parental incubation regime that lead to lethal chilling or heating of the eggs, or from mechanical destruction (Webb 1987). Embryos can also die because of infection with pathogenic microorganisms or contamination with toxic substances (Jopek et al. 1995, Pinowski et al. 1995ab). What can thus be the role of factors affecting egg failure such as egg mass, length, and breadth? Embryos in small eggs may have died from insufficient reserves to complete normal development (Bolotnikov et al. 1978, 1985, Royle et al. 1999). Small eggs may have too thick shell, and this combined with lower energy resources can lead to the death of embryos during hatching (Murton et al. 1974). Ojanen (1983b) and Ankney & Johnson (1985) found that egg weight was a good predictor of energy content in eggs of the Pied Flycatcher *Ficedula hypoleuca*, Great Tit, and Brown-headed Cowbird *Molothrus ater*. An increase in egg size for an altricial bird is associated with a disproportionate increase in wet albumen. In contrast, wet yolk display negative allometry for altricial birds (Ojanen 1983c, Hill 1995). Depending on the sequence of laying and egg size, the content of vitamin A and carotenes in egg yolk vary. In the Rook *Corvus frugilegus*, the ratios of egg mass, yolk, carotenes, and vitamin A in the last and first-laid eggs were 0.91, 081, 0.55, and 0.39, respectively (Bolotnikov et al. 1978). Similar relationships in the contents of vitamins A and E and carotenes was found in gulls (Royle et al. 1999). The content of carotenes and vitamin A is of fundamental importance to the survival of embryos (Bolotnikov et al. 1978). Deficiency in vitamin E accounts for the death of embryos already at the beginning of incubation (Royle et al. 1999). Small eggs may cool more rapidly during parental absences with adverse effects on embryo, however according to O'Connor (1979) small differences in cooling rate between large and small eggs is not likely to affect hatchability. But under extreme conditions, this may affect hatchability (Järvinen & Väisänen 1983). Low temperatures below "physiological zero" can kill embryos, but temperatures between "physiological zero" (changing with the age of embryo) and optimum temperatures they cause developmental defects affecting hatchability (Webb 1987). In our study, we classified dead embryos to three age groups (see Methods). The number of "infertile" eggs was the highest and the number of dead embryos was the lowest during hatching (Table 2). We examined in detail the effect of temperature on egg size (B. Pinowska et al., unpubl. ms., J. Pinowski et al., unpubl. ms.). High temperatures as well as low temperatures explain only a few percent of the variation in egg mass. Their effect on hatchability may be similar. We found no relationship between hatching rate and the sequence of laying in the Tree Sparrow, but we observed a tendency to the hatching failure of the first and last eggs (Fig. 3), also observed in other bird species (Potti & Merino 1996). We found a significant difference in egg breadth between clutches with full hatching success, and deserted clutches and between fully successful clutches (that is, fertile) and "infertile" eggs. (Table 3). Potti & Merino (1996) found significant differences not only in egg breadth but also in egg length between fully successful and partially successful clutches of Pied Flycatcher. We have not found relationship between the hatching rate of Tree Sparrow eggs and the shape index B/L (Table 3), confirming the results obtained by Encabo et al. (2001) for Great Tit and Blackbird. The hatchability of rounded eggs of Cape Petrel *Daption capense* was higher than the hatchability of long eggs, but not significantly so (Weidinger 1996).

In Tree Sparrow we have not found a relationship between hatching rate and the sequence of laying. This does not support the hypothesis (egg-viability hypothesis) that reduced hatchability of early-laid eggs could be due to greater temporal exposure to environmental factors (Veiga & Viñuela 1993), nor the hypothesis of reserve depletion for explaining failure late in the laying sequence. Cordero et al. (2000) found that House Sparrow eggs producing males are larger by 1.3 % than the eggs producing females, and he doubts whether such a small difference in egg size can affect nestling or juvenile mortality. We do not know whether this is valid for Tree Sparrow. Differences in egg mass among fully successful, partially successful, and "infertile" eggs, although small, are significant. Thus, it is very likely that sex-related differences in egg size, if present in Tree Sparrow eggs, can influence hatchability. Most papers on the effect of egg size on hatchability are focused on small eggs. Jones (cited in Ojanen 1983a), however, found a lower hatchability of both small and very large eggs of Great Tit, like in poultry (see Ojanen 1983a for review). We did not find such tendency in Tree Sparrow.

Larger eggs produce larger nestlings that have a higher probability of survival (see Williams 1994 for review). This could provide a selection force in favour of large eggs. On the other hand, selection for small eggs might result from benefits for the female investing less energy in egg formation (van Noordwijk et al. 1981). A female investing less energy and nutrients in egg production should be in better condition during incubation and rearing nestlings, and she could raise more broods in a season as well as in next years, and overwinter in a higher percentage.

In this paper we found evidence that egg size affected hatching rate in Tree Sparrow. But to what extent does it affect population fitness? Preliminary results (data of J. Pinowski et al.) show that egg mass has a positive effect on growth rate of Tree Sparrow nestlings only for the first four days of life.

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STRESZCZENIE

[Wpływ wielkości jaja na sukces wykluwania u mazurka w centralnej Polsce]

Badania prowadzono na terenie wsi położonych pomiędzy Wisłą a Kampinoskim Parkiem Narodowym, około 15km NW od Warszawy (52°20′ N, 20°50′ E). W latach 1994 i 1995 w czasie okresu lęgowego codziennie kontrolowano 200 skrzynek lęgowych. Znakowanie jaj w dniu złożenia umożliwiło ustalenie kolejności składania jaj. Mierzono długość (L) i maksymalną szerokość (B) jaj. W 1995 roku jaja były również ważone. Wyliczono równanie regresji opisujące zależność masy jaja (M) od jego długości i szerokości zgodnie ze wzorem:

$$M = 0.000546 \times L \times B \ (r = 0.90, p < 0.001)$$

Aby zachować możliwość analizy materiału z obydwu lat łącznie masę jaj wyliczono dla całego materiału.

W okresie wykluwania kontrolowano skrzynki tak często aby identyfikować jajo z wyklutym pisklęciem. W obu latach badań analizowano 257 zniesień w tym 115 z pełnym sukcesem wyklucia, 118 z częściowym i 25 zniesień opuszczonych (Tab. 1). W zniesieniach tych złożone były 1332 jaja z których wykluły się 1053 pisklęta, a przyczynami niewyklucia się piskląt były: nie zapłodnienie jaja, śmierć zarodka, śmierć pisklęcia w czasie wykluwania (Tab. 2).

Oceniono (po wyeliminowaniu źródeł zmienności wywołanych powtarzalnością masy jaj w zniesieniu i zmienności masy zależnej od kolejności składanego jaja) różnice średnich mas jaj, średnich ze średniej masy jaja w zniesieniu, oraz średnich odchyleń mas od wzorca w lęgach o pełnym sukcesie wyklucia, częściowym i w lęgach opuszczonych stosując analizę wariancji (ANOVA), dwuczynnikową analizę wariancji (Two-way ANOVA) i test LSD.

Gniazda o pełnym, częściowym sukcesie wyklucia oraz opuszczone różniły się pod względem wielkości zniesień (Fig1). W grupie zniesień o wielkości 4-6 jaj wzrostowi średniej masy jaja w zniesieniu odpowiada istotny wzrost liczby zniesień o większym sukcesie wyklucia (Fig 2).

Średnia masa jaj z lęgów o pełnym sukcesie klucia była większa od średniej masy jaj wyklutych ze zniesień o częściowym sukcesie klucia oraz masy jaj z zamarłym zarodkiem i niezapłodnionych (ANOVA: F = 2,318, p < 0,05; Tab. 3). Średnie masy jaj w zniesieniach 4-, 5- i 6-jajowych rosły do przedostatniego jaja (Fig. 3), ale istotnie różniły się tylko średnie masy jaj o różnym sukcesie wyklucia w zniesieniach zawierających 5 jaj (Fig. 3 B)

Odchylenia masy kolejnych jaj od średniej masy jaj danej wielkości zniesienia (Tab. 4) w obrębie jaj pochodzących ze zniesień o pełnym sukcesie wyklucia były mniejsze niż w niepełnym i bez sukcesu (Tab. 5). Jaja o pelnym sukcesie wyklucia mialy większą średnicę (ANOVA: F = 2.233, p < 0,05) niż niezapłodnione Tab. 3).

U mazurka jaja mniejsze mają mniejszą szansę wyklucia i tym samym zwiększają możliwość eliminacji samic, które z różnych powodów składają takie jaja.