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Repeatability of egg dimensions within the clutches of Bearded Tit *Panurus biarmicus*

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Abstract. The variation in size and shape of Bearded Tit eggs was investigated in the Wielkopolska Region of western Poland in 1988–1992 and 1997–2000. The mean clutch size was 5.47 (95% CL: 5.25–5.70, n = 99), and differed markedly from year to year. Coefficients of variations for the mean egg characteristics in a clutch ranged from 1.91 (breadth) to 4.90 (volume). No significant correlation between egg length and breadth was found. Repeatability estimates were 0.50, 0.48, 0.50, 0.47 for length, breadth, volume and elongation index, respectively. The results suggest a relatively low heritability of egg dimensions in the population studied.

Key words: Bearded Tit, *Panurus biarmicus*, egg size, clutch size, repeatability of egg dimensions, biometry

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INTRODUCTION

The size of bird eggs may be important in determining body size and condition of fledglings, their probability of survival and, ultimately, their reproductive success (Schifferli 1973, Williams 1994). Variation in egg dimensions results from both genetic determination and impact of environmental conditions on these features. Obtaining measurements necessary for determining heritability (h^2) values is difficult in most bird species in the wild (Boag & van Noordwijk 1987, Bańbura & Zieliński 1990). However, repeatability is relatively easy to estimate and provides an upper limit for the degree of genetic determination and heritability (e.g., Boag & van Noordwijk 1987, Bańbura & Zieliński 1990, Falconer & Mackay 1995). On the other hand, low values of repeatability can indicate a significant environmental component in the phenotypic variance (Bańbura & Zieliński 1998).

There were some studies on egg dimensions in the Bearded Tit, however, they are mainly descriptive and do not provide any analysis of phenotypic variation (c.f. Wawrzyniak & Sohns 1986). To date, repeatability of egg dimensions has been studied only in a few small Passerines, mainly hole-nesting species (Ojanen et al. 1979, van Noordvijk 1987). Studies on repeatability of egg dimensions in ground, open nest species are exceptionally rare (but see Hendricks 1991), while data from marshland species are completely lacking. In this study we investigated phenotypic variation in traits associated with egg size (length, breadth, volume and index of elongation) in a stable population of the Bearded Tit.

We made an attempt to assess an influence of environment (*sensu* Bańbura & Zieliński 1998) on eggs measurements using repeatability estimates.

STUDY AREA AND MATERIALS

This study was carried at Łoniewskie Lake and Zgliniec Ponds (51°54’N, 16°41’E), near Osieczna, western Poland. Dominant littoral types of vegetation were reeds and bushes. For more details of the study area see Kuźniak & Lorek (1993) and Stępniewski (1995).

The data were collected during 9 breeding seasons, (1988–1992 and 1997–2000). Nest sites were located by following adults who carried building materials, than they were controlled at the late stage of incubation. A total of 100 nests with complete clutches were found.

Data processing and analysis

Seven clutches were excluded from analysis of the influence of clutch size on egg differentiation because of small sample sizes in some extreme clutch classes. These were: 1 clutch with 3 eggs, 3 with 8 and 2 clutches with 9 eggs. Also one clutch with 7 eggs was excluded from further egg size analyses because it included one extremely small egg, a runt egg (11.6 × 9.7 mm). This procedure was performed following Zar's (1999) suggestion on sample homogeneity. Another clutch of 12 eggs was not used in analyses, because of evident brood parasitism (Stępniewski 1995). Moreover, in 1988 and 1989 only 6 nests were found. Therefore these years were not considered in the analysis of differences in clutch size between years and they were excluded from the repeatability analysis.

The length (L) and breadth (B) of eggs in complete clutches were measured by the same person (J. Stępniewski) with callipers to the nearest 0.1 mm. Egg volume (V) in cm^3 was estimated following Hoyt's (1979) formula: $V = 0.00051 \times L \times B^2$. An index of egg elongation was calculated as the ratio of egg length to egg breadth. Within-clutch coefficient of variation of egg measurements (using formula of adjusted *CV** for small sample sizes (Sokal & Rohlf 1995) and repeatability of egg measurements (Lessells & Boag 1987, Falconer & Mackay 1995) were also calculated. Standard errors for repeatability values were calculated as described in Becker (1992). Mean values of all egg characteristics in the clutch were used as unit observations throughout this paper to avoid pseudoreplication (Lessells & Boag 1987). Throughout the text, we use the abbreviation CL for the 95% confidence limits.

RESULTS

Bearded Tit clutches (n = 99) contained from 3 to 9 eggs. Mean clutch size was 5.47 (CL: 5.25–5.70), modal clutch size was 5 (Fig. 1). The clutch size differed significantly among years of study (Kruskal-Wallis ANOVA, $H_6 = 15.96$, n = 92, p = 0.014, Fig. 2).

Correlation coefficient between mean egg length and mean egg breadth was not different from zero (r = 0.052, n = 99, p = 0.613, Table 1).

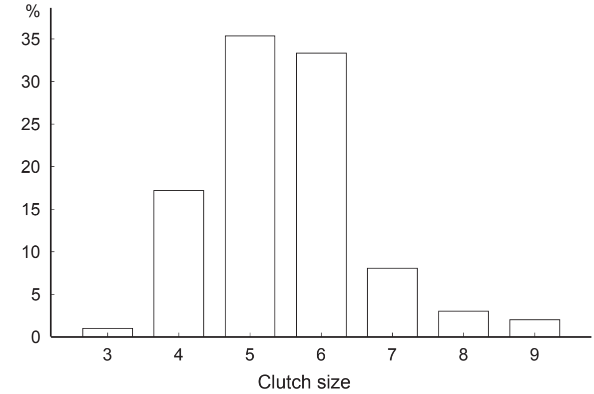

Fig. 1. Frequency distribution of clutch size in Bearded Tit nests (N = 99).

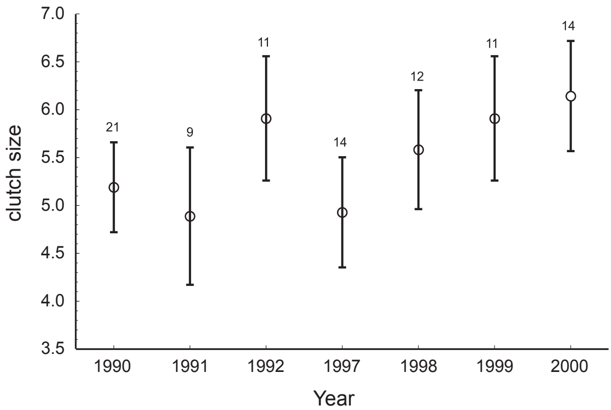

Fig. 2. Mean clutch size with 95% confidence limits.

No significant differences (One-way ANOVA test) in egg dimensions were found between clutch size classes and egg length ($F_{3,89} = 1.77$, p = 0.158), breadth ($F_{3,89} = 0.15$, p = 0.929), volume ($F_{3,89} = 0.18$, p = 0.91) and elongation index ($F_{3,89} = 1.81$, p = 0.15).

The highest within-clutch variation (n = 99) was recorded for egg volume CV* = 4.60 (CL: 4.06–5.15; range: 0.40–18.50), then for the elongation index CV* = 3.25 (CL: 2.81–3.69; range: 0.49–13.42), egg length CV* = 2.58 (CL: 2.27–2.90; range: 0.26–11.63) and egg breadth CV* = 1.91 (CL: 1.64–2.18; range: 0.37–10.54).

The coefficient of within-clutch variation differed significantly for egg dimensions (Friedman ANOVA; $\chi^2 = 133.74$, df = 3, n = 99, p < 0.00001).

No significant differences between within-clutch coefficients of variation for different clutch size classes were found for egg volume (Kruskal-Wallis ANOVA, $H_3 = 2.22$, n = 93, p = 0.528).

Table 1. Egg measurements — means of clutch, its range and range for all eggs.

Parameter	Clutch (95% CL) (N = 99)	Range (N = 99)	All eggs (N = 542)
Length (mm)	18.06 (17.94–18.17)	15.94–19.87	15.00–23.30
Breadth (mm)	14.38 (14.31–14.45)	13.50–15.22	11.90–15.80
Volume (cm^3)	1.91 (1.88–1.93)	1.48–2.18	1.26–2.33
Elongation	1.26 (1.25–1.27)	1.16–1.42	1.04–1.66

The repeatability estimates for eggs measurements did not differ among years of study (Fig. 3). Repeatability estimates ranged from 0.47 to 0.50 (Table 2).

Table 2. Repeatability (r) of egg measurements. All F-ratios (one-way ANOVA) have $p < 0.001$ significance.

Parameter	F	df	r	95% CL
Length	6.47	91, 405	0.50	0.41–0.60
Breadth	6.02	91, 405	0.48	0.39–0.58
Volume	6.52	91, 405	0.50	0.41–0.60
Elongation	5.88	91, 405	0.47	0.38–0.57

DISCUSSION

The mean clutch size recorded in this study does not deviate markedly from values found in other European populations (Wawrzyniak & Sohns 1986, Cramp 1998). Larger clutches were recorded in the Netherlands and Hungary, while similar clutch sizes were reported from Russia and Germany (Wawrzyniak & Sohns 1986). Being consistent with conclusions of Cramp (1998), our data do not provide any new evidence for the geographical variation in the Bearded Tit clutch size. This seems obvious, since Bearded Tit subpopulations are extremely mobile and certainly

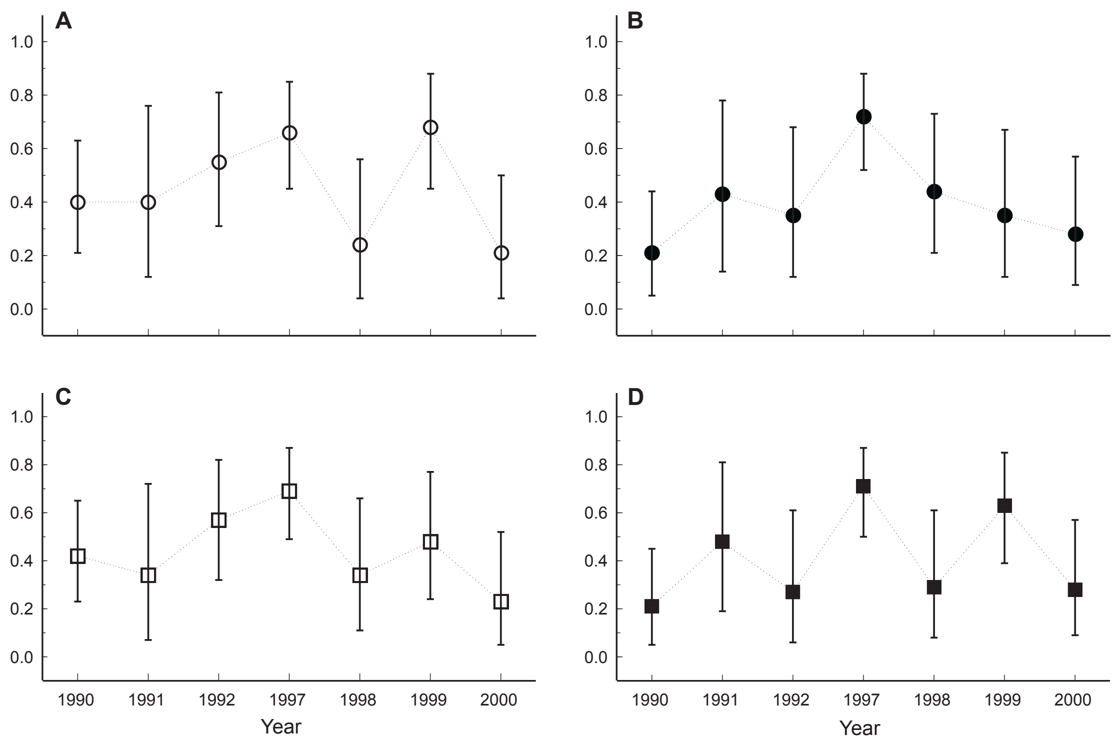

Fig. 3. The repeatability estimates with 95% confidence limits for length (A), breadth (B), volume (C) and elongation index (D).

mix throughout the species range (Cramp 1998). In addition, our results indicated that clutch size may significantly changes from year to year (Fig. 2).

Unfortunately, no data on volume and elongation index in other Bearded Tit populations are available. Mean length and breadth in the studied population are among the highest values recorded in Europe (Wawrzyniak & Sohns 1986). Only two populations (out of twelve studied) reached length and breadth equal or exceeding 18.0 and 14.3 mm respectively (Wawrzyniak & Sohns 1986). These differences seem not to be biologically significant and may arise from local and temporal changes in weather and/or food resources. These factors probably influence egg measurements to a greater extent than the number of eggs in a clutch and thus there is a lack of a trade-off between egg and clutch size.

Egg measurements differ in their within-clutch variation. The greatest variation was recorded in egg volume, the lowest for egg breadth. This observation seems to represent a more general rule and has been reported for many bird species (review in Ojanen 1983, Bańbura 1996, Tryjanowski et al. 2001). Low variation in egg breadth may result from the fact that this variable is more constrained by the female oviduct diameter (van Noordwijk et al. 1981). Thus, maximisation of egg volume may be achieved easier by increasing egg length which is less limited by physiological or mechanical conditions. The high variation in egg volume is connected with the fact that volume increases approximately to the cube of linear measurements of the egg. Hence, the largest eggs in a population may have a two times larger volume than the smallest one. The greatest variation in egg volume and shape is also probably due to the variance accumulation resulting from computational formulas. Both parameters are calculated in such a manner that they inherently contain cumulated variance of input variables (Bańbura 1996).

A correlation between egg length and egg breadth is a common phenomena among passerine species (Järvinen & Pryl 1989, Tryjanowski et al. 2001, Zduniak & Antczak 2003). Our study provides evident exception from this rule (but see Bańbura 1996 on methodological bias). The evolution of egg dimensions is complicated by the fact, that both egg length and egg breadth may be under strong selection acting for each trait independently and possibly in opposite directions (Chylarecki 1993, Bańbura 1996, Barta & Szekely 1997, Chylarecki et al. 1997). Besides the egg volume, egg shape (understood as a proportion of egg length to egg breadth) may also influence fledgling condition (Barta & Szekely 1997). To maximise it, a female maintain some optimal, species-specific ratio of egg length to egg breadth which results in a correlation between these two values. In the Bearded Tit, however, one pair may produce up to 4 regular clutches yearly (Stępniewski 1995, Cramp 1998). Thus, in this case a large number of eggs rather than their shape is the main strategy of increasing breeding success.

The repeatability estimates for egg parameters of the Bearded Tit (0.47–0.50) are markedly lower than values calculated for small passerine birds (Boag & van Noordwijk 1987, Hendricks 1991, Potti 1993, Bańbura 1996) and larger species like corvids as well (Jerzak et al. 2000, Tryjanowski et. al 2001, Zduniak & Antczak 2003). Low values of repeatability in the Bearded Tit eggs dimensions indicates that they are strongly influenced by environmental factors while genetic components of variation are relatively low. We suggest that this is an adaptation to both long reproduction time and site-specific conditions. Breeding season in Bearded Tits last on average about 130 days (Stępniewski 1995). During that time conditions in marshes changes completely in terms of water level, vegetation cover and density and potential food resources (Dyrcz & Zdunek 1996). At such circumstances low heritability of egg dimensions rather than high would be expected. Species whose egg repeatability has been reported to date breed once or twice a year, build cavity nests or inhabit urban habitats (van Noordvijk 1984, Potti 1992, Bańbura & Zieliński 1998, Jerzak et al. 2000, Tryjanowski et al. 2001). All these factors may make them partially independent of environmental conditions and explain relatively high repeatability of eggs dimensions.

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REFERENCES

Bańbura J. 1996. [Intrapopulation variability of egg measurements in the Barn Swallow *Hirundo rustica*]. Wyd. UŁ., Łódź.

Bańbura J., Zieliński P. 1990. Within-clutch repeatability of egg dimensions in the Black-headed Gull *Larus ridibundus*. J. Ornithol. 131: 305–310.

Bańbura J., Zieliński P. 1998. An analysis of egg-size repeatability in Barn Swallows *Hirundo rustica*. Ardeola 45: 183–192.

Barta Z., Szekely T. 1997. The optimal shape of avian eggs. Funct. Ecol. 11: 656–662.
Becker W. A. 1992. Manual of Quantitative Genetics. Academic Enterprises, Pullman, Washington.
Boag P. T., van Noordwijk A. J. 1987. Quantitative genetics. In: Buckley P. A., Cooke F. (eds). Avian genetics. Academic Press, London, pp. 45–78.
Chylarecki P. 1993. Decomposing selection on avian egg size. Proc. IVth Congr. Europ. Soc. Evol. Biol., Montpellier, p. 82.
Chylarecki P., Kuczyński L., Vorgin M., Tryjanowski P. 1997. Geographical variation in egg measurements of the Lapwing *Vanellus vanellus*. Acta Ornithol. 32: 137–148.
Cramp S. 1998. The complete Birds of Western Palearctic on CD-ROM. Oxford Univ. Press.
Dyrcz A., Zdunek W. 1996. [Potential food resources and nestling food in the Great Reed Warbler *Acrocephalus arundinaceus* and Reed Warbler *Acrocephalus scirpaceus* at Milicz fish-ponds]. Ptaki Śląska 11: 123–132.
Falconer D. S., Mackay T. C. F. 1995. Introduction to quantitative genetics. Longmann, Harlow.
Hendricks P. 1991. Repeatability of size and shape of American Pipit eggs. Can. J. Zool. 69: 2624–2628.
Hoyt D. F. 1979. Practical methods for estimating volume and fresh weight of birds eggs. Auk 96: 73–77.
Järvinen A., Pryl M. 1989. Egg dimensions of the Great Tit *Parus major* in southern Finland. Ornis Fenn. 66: 69–74.
Jerzak L., Bocheński M., Kuczyński L., Tryjanowski P. 2000. Repeatability of size and shape of eggs in the urban Magpie *Pica pica* (Passeriformes: Corvidae) population. Acta zool. Cracov. 43: 165–169.
Kuźniak S., Lorek G. 1993. [Birds of Wonieść Reservoir and surrounding areas (Western Poland)]. Prace Zakł. Biol. i Ekol. Ptaków UAM 2.
Lessells C. M., Boag P. T. 1987. Unrepeatable repeatabiles: a common mistake. Auk 104: 116–121.
Ojanen M. 1983. Significance of variation in egg traits in birds, with special reference to Passerines. Acta Univ. Oulu 154 A, Biol. 20: 1–61.
Ojanen M., Orell M., Vaisanen R. A. 1979. Role of heredity in egg size variation in the Great Tit *Parus major* and Pied Flycatcher *Ficedula hypoleuca*. Ornis Scand. 10: 22–28.
Potti J. 1993. Environmental, ontogenetic, and genetic variation in egg size of Pied Flycatchers. Can. J. Zool. 71: 1534–1542.
Schifferli L. 1973. The effects of egg weight on the subsequent growth of nestling Great Tits *Parus major*. Ibis 138: 2–15.
Sokal R. R., Rohlf F. J. 1995. Biometry. Freeman, New York.
Stępniewski J. 1995. Ausgewählte Aspecte der Brutbiologie der Bartmeise *Panurus biarmicus*: Beobachtungen am Loniweskie-See in West-Polen. Vogelwelt 116: 263–272.
Tryjanowski P., Kuczyński L., Antczak M., Skoracki M., Hromada M. 2001. Within–clutch repeatability of egg dimensions in the jackdaw *Corvus monedula*: a study based on a museum collection. Biologia, Bratislava 56: 211–215.
Van Noordvijk A. J. 1987. Quantitative ecological genetics of great tits. In: Cooke F., Buckley P. A. (eds). Avian genetics. Academic Press, London, pp. 363–380.
Van Noordwijk A. J., Keizer L. C. P., van Balen J. H., Scharloo W. 1981. Genetic variation in egg dimensions in natural populations of Great Tit. Genetica 55: 221–232.
Wawrzyniak H., Sohns G. 1986. Die Bartmeise. Die Neue Brehm–Bücherei. A. Ziemsen Verlag, Wittenberg Lutherstadt.
Williams T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. Biol. Rev. 68: 35–59.
Zar J. H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, New Yersey.
Zduniak P., Antczak M. 2003. Repeatability and within-clutch variation in egg dimensions in a Hooded Crow *Corvus corone cornix* population. Biol. Lett. 40: 37–42.

STRZESZCZENIE

[Powtarzalność wymiarów jaj u wąsatki]

Badania prowadzono w latach 1988–1992 oraz 1997–2000 w okolicach Osiecznej (powiat Leszczyński, południowa Wielkopolska). Analizowano 4 parametry wymiarów jaj: długość (L), szerokość (B), objętość (V) oraz współczynnik kształtu (S). Objętość była szacowana na podstawie wzoru: $V = 0.51 \times L \times B^2 / 1000$ (Hoyt 1979) i wyrażona w cm^3. Współczynnik kształtu jaj został wyrażony jako stosunek długości (L) do szerokości (B). W celu uniknięcia efektu pseudoreplikacji, w analizach zastosowano średnie wartości wymiarów jaj dla poszczególnych zniesień (Lessells & Boag 1987). Odziedziczalność rozmiarów jaj obliczono z wykorzystaniem współczynnika powtarzalności *r* (Sokal & Rohlf 1995).

Wielkość zniesienia (n = 99) wahała się między 3 a 9. Średnia wartość zniesienia wynosiła 5.47 (95% CL: 5.25–5.70), zaś jego wartość modalna — 5 (Fig. 1). Nie stwierdzono istotnej korelacji między długością a szerokością jaj. Największą wariancję w obrębie zniesienia odnotowano dla objętości (4.60), później dla współczynnika kształtu (3.25), długości (2.58) i szerokości jaj (1.91). Powtarzalność wymiarów jaj nie różniła się istotnie między latami (Fig. 3). Średnie wskaźniki powtarzalności dla długości, szerokości, objętości i współczynnika kształtu jaj wynosiły odpowiednio: 0.50, 0.47, 0.50, 0.47 (Tab. 2).

Powtarzalność wymiarów jaj w badanej populacji wąsatki jest niska w porównaniu z innymi badanymi wcześniej ptakami wróblowymi (Hendricks 1991, Potti 1993, Bańbura 1996, Tryjanowski et al. 2001). Świadczy to o tym, że wymiary jaj wąsatek były tylko w niewielkim stopniu cechą odziedziczalną, natomiast silnie kształtowaną przez warunki środowiskowe. Strefa litoralna zbiorników wodnych gdzie występuje wąsatka, podlega znaczącym zmianom stanu wody, zasobów pokarmowych i roślinności. Znaczenie ma też długi (średnio 130 dni) sezon lęgowy u tego gatunku.