

REPEATABILITY ANALYSIS OF EGG SHAPE IN A WILD TREE
SPARROW (*PASSER MONTANUS*) POPULATION:
A SENSITIVE METHOD FOR EGG SHAPE DESCRIPTION

MÓNUS, F. and BARTA, Z.

*Behavioural Ecology Research Group, Department of Evolutionary Zoology
University of Debrecen, Debrecen H-4010, Hungary, E-mail: monusf@delfin.unideb.hu*

The shape of avian eggs varies widely among and within species. To explore this variation, several methods for egg shape description were used in previous works. The simplest methods were unsuitable to detect small differences in shape of different eggs, while more elaborated methods required special equipment, since they were not generally used. In this study we present a simple method for egg shape description which incorporate quickness in the field, high sensitivity to egg shape differences and furthermore require no special equipment. The method is based on a function which describe the outline of the egg in a two dimensions co-ordinate system and outline originates from field taken photographs. The method was tested on clutches of wild living Tree Sparrow (*Passer montanus*) population. Three out of four parameters of the function were found to be repeatable in Tree Sparrows. The eggs of repetitive clutches of females were more similar considering these egg shape parameters than eggs of different females. A simple, widely used index to describe egg shape, egg shape index was found to be far less sensitive in our repeatability analyses. The method described here may be particularly suitable to investigate intraspecific variation of egg shape.

Key words: egg shape, description, repeatability, Tree Sparrow, *Passer montanus*

INTRODUCTION

Shape of bird eggs become frequently in the field of interest of researchers. Shape may be contribute in solidity of the egg (BAIN 1991, BAIN & SOLOMON 1991), may affect gas transfer (AR *et al.* 1974) or the effort needed to manage eggs in a given shaped nest cup by the incubating parent (ERÓSS 1983). Egg shape may also have adaptive significance allowing to individual eggs to obtain the largest possible volume according to species specific clutch size when the surface of overall clutch is limited by female incubating patch (DRENT 1975, ANDERSSON 1978, BARTA & SZÉKELY 1997). While larger egg volume may result in enhanced survival (WILLIAMS 1994, AMAT *et al.* 2001). Egg shape was also found to be a useful trait to identify intraspecific parasitic eggs in a study of Emperor Geese (PETERSEN 1992), which suggests that small intraclutch egg shape variation relative to interclutch variation may be adaptive for birds to avoid inter- or intraspecific nest parasitism as it was assumed in case of other visual traits of egg appearance, such as colour and marking pattern (BROWN & SHERMAN 1989, OIEN *et al.* 1995,

STOKKE *et al.* 2002, see also MOSKÁT *et al.* 2002). All these evolutionary processes are hypothesized to result in the great interspecific and in some species, the important intraspecific observed variation of egg shape (PRESTON 1969, MÄND *et al.* 1986, PETERSEN 1992). These processes are poorly investigated; one of the main reasons of this is the difficulty of egg shape description.

For statistical analyses it is necessary to characterise egg shape quantitatively. Previous work usually described egg shape with parameters derived from length and breadth, e.g. egg shape index (maximum breadth per length; HICKS 1958, CARTER & JONES 1970, MÄND *et al.* 1986, BROWN & SHERMAN 1989, PETERSEN 1992, HORAK *et al.* 1995, TSERVENI-GOUSI & YANNAKOPOULOS 1995) or elongation index (length per maximum breadth; GRANT 1982, HENDRICKS 1991, PETERSEN 1992, OLSEN *et al.* 1994). Because the latter is the reciprocal of the former and there is no functional difference between them, both will be referred to as egg shape index (*ES*) throughout this paper. Although some papers use more elaborate indices derived from measurements performed by a spherometer (PRESTON 1953, 1968, 1969) or from various distances between specific points taken from egg photos (MÄND *et al.* 1986, PETERSEN 1992), *ES* remains the most widely used parameter because it is easy to measure. On the other hand, eggs described with the same *ES* can be of totally different shapes, as illustrated in Figure 1 (see also Fig. 5 in PRESTON 1969). Consequently *ES* may be insufficient to study egg shape quantitatively.

In this study our aims are twofold. First, we look for among female and within female variability of egg shape in a wild Tree Sparrow population by the means of repeatability analyses (LESSELS & BOAG 1987, FALCONER 1989, HENDRICKS 1991). Second, to do so, we test a more elaborate egg-shape description method to eliminate the insensitivity of previous methods based on egg breadth and length, requiring no spherometer, graphics pad or other special equipment and data collecting could be very fast in the field resulting in the less possible disturbance on the studied individuals and their eggs.

METHODS

This study was conducted on European Tree Sparrows, *Passer montanus m.*, in the Botanical Garden of the University of Debrecen (formerly Kossuth University), Hungary, during the summers of 1998 and 1999. Tree sparrows have been reported nesting in the Garden for decades (BOZSKO 1968, BOZSKO & PAPP 1980). They frequently occupy artificial nest boxes and lay two or three clutches per year each containing four to six eggs (SUMMERS-SMITH 1995). Since a Tree Sparrow female usually uses the same nest for her consecutive clutches within a year and during the following years (SUMMERS-SMITH 1995), we treated consecutive clutches found in the same nest box as the clutches of the same female. To check for nest faithfulness in our study site, we have been marking

Tree Sparrows in the Garden by unique combination of colour rings since March 1998 and regularly surveyed birds using the studied nest-boxes.

Length and breadth of eggs found in the nest boxes were measured and each clutch was photographed together with a scale. Photographs were taken from the same distance with a 35-mm camera and with a lens of 50 mm focal length. A special egg-holding platform, a special support for the camera (similar accessories are described in detail in MÄND *et al.* 1986) and a macro-ring flash were used to standardise the conditions of photography. Eggs were always tried to place on the platform in such a way that its equatorial plan is parallel to the platform. We used these photos to determine the outline of eggs by measuring their length, maximal breadth, and nine other breadths on the photos (Fig. 2). These nine breadth measurements were taken so that they divided the long axis of the eggs in ten intervals of roughly equal length (Fig. 2). Measurements were made using different methods in the two years. In 1998, egg photographs were adjusted to the same magnification by photocopying and measurements were performed manually (accuracy: 0.1 mm) with a calliper from these copies. In 1999, photos were digitalized with a Nikon MSZ-2T camera and measurements were performed with the help of NIH Image 1.44 for Macintosh (accuracy: 0.05 mm).

Egg shape was described by means of the following function, in such a way that the longitudinal axis of the egg always lies on the x axis (TODD & SMART 1984):

$$f(x) \rightarrow Y = \pm\sqrt{a^2 - X^2}(c_0 + c_1x + c_2x^2 + c_3x^3) \quad (1)$$

where $2a$ is the length of the egg, X, Y gives the co-ordinates of outline points and $x = X/a$. The function has four parameters, i.e. c_0, c_1, c_2 and c_3 . $2ac_0$ gives the equatorial breadth of the egg. With increasing c_1 egg shape becomes more pointed, c_1 and c_3 determine asymmetry of the egg, while c_2 determines the bicone character (PRESTON 1968) of the egg. The parameters c_1, c_2 and c_3 are similar to that, which were used by PRESTON (1953, 1968, 1969) to calculate asymmetry, bicone and alcity, nevertheless PRESTON used polar coordinates to determine egg shape.

Egg shape was quantified by finding those values of c_0, c_1, c_2 and c_3 parameters that give the best fit of the function to the outline points. Assuming the egg symmetric along the line of maximal length, parameters were calculated from data collected from the photographs using the computer algorithm of PRESS *et al.* (1992) for multivariate least square fitting. Besides the above-mentioned parameters, ES of each egg was also calculated, since ES is widely used in the literature regarding egg shape (see in Introduction).



Fig. 1. Differently shaped eggs characterised with the same egg shape index ($ES = 0.7$)

To compare intra- and inter-individual variation repeatability analyses were used (FALCONER 1989, RIDLEY 1993). Repeatability (r) divides phenotypic variance (V_p) of a trait into among- and within-individuals variation in a given population. It shows the proportion of genetic (V_G) and general environmental (V_{Eg}) variance to total phenotypic variance excluding the special environmental variance (V_{Es}) from the numerator (FALCONER 1989):

$$V_p = V_G + V_{Eg} + V_{Es} \quad (2)$$

$$r = (V_G + V_{Eg}) / V_p \quad (3)$$

We estimated repeatability based on two markedly different statistical designs. A hierarchical, nested ANOVA was recently proposed to use uniquely (FLINT *et al.* 2001) when estimating repeatability values of egg parameters. Being widespread, repeatability estimated from one-way ANOVA (HENDRICKS 1991, PETERSEN 1992) is also published to make our results comparable to previous studies. In this latter case groups in the ANOVA consist clutch-averages of the trait of consecutive clutches laid by the same female. This way of calculation may not consider both within-female within clutches and within-female among clutches variability of trait, accordingly excludes within-clutch variation from the analyses and may inflate repeatability estimates (FLINT *et al.* 2001). However, the hierarchical method considers all three possible sources of variation, i.e. within clutch, within female and among females variation (BANBURA & ZIELINSKY 1998, FLINT *et al.* 2001).

Repeatabilities were calculated according to LESSELS & BOAG (1987). Standard error of repeatability was calculated following BECKER (1984). Samples of the two years cannot be considered as independent samples, because females may occur in both samples (as one of the marked females does). In the case of unmarked females we cannot be sure that we excluded repeated sampling of the same female, thus, we treated data of the two years separately. Statistical analyses were performed using SPSS 9.0 for Windows.

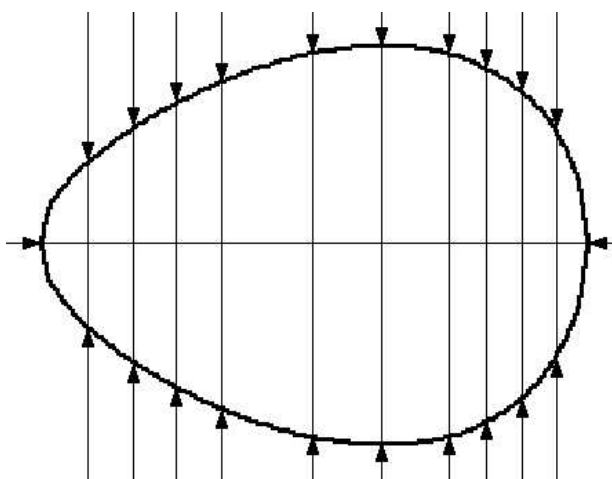


Fig. 2. Data collecting method results in 22 co-ordinates of each eggs

RESULTS

We examined 15 clutches (68 eggs) from eight nest boxes and 9 clutches (45 eggs) from four nest boxes in 1998 and 1999, respectively. Since Tree Sparrow is a nest-faithful species (SUMMERS-SMITH 1995), we considered the clutches found in one box, as the clutches laid by the same female. This statement is also supported by our observations. Colour ringing allowed us to identify three females in 1998 and one in 1999 out of the females included in this study. All of them used the same nest box for the consecutive clutches.

First we tested our sampling and measuring method. Placing the egg on the platform during photographing did not affect seriously the outline of the egg (Fig. 3). To estimate the measurement error, three sets of measurements were performed on five randomly selected egg photos in both years. Regarding the extracted parameters, ANOVA shows significant difference between the parameters of different eggs, which means that the measurement error does not hide the differences between egg shapes (Table 1). We compared length and breadth measured in the field and the derived egg shape indices to those collected from photos. Though both length and breadth measurements taken in the field were significantly higher than those derived from the photos (paired t-tests; length: $t = 2.04$, $df = 67$, $p = 0.045$; $t = 31.43$, $df = 44$, $p < 0.001$; breadth: $t = 2.36$, $df = 67$, $p = 0.021$; $t = 21.83$, $df = 44$,

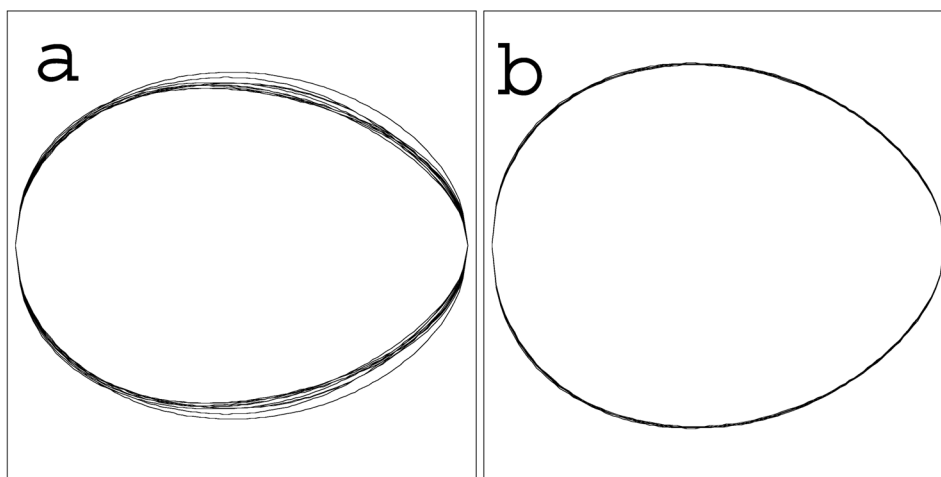


Fig. 3. The effect of egg-photographing on the description of outline. Panel *a* shows ten outlines described following the photos of ten randomly chosen eggs, panel *b* shows ten outlines described following ten different photos of one randomly chosen egg

Table 1. The accuracy of egg shape measurements. Results of comparison by ANOVA (df = 4 and 10; MS_A and MS_W are the among-group and the within-group variances, respectively) and repeatability analyses (r) of three sets of measurements made on five randomly selected eggs

parameter	year	MS_A	MS_W	F-ratio	P	$r \pm SE$
c_0	1998	0.0046	0.0001	91.65	0.0000	0.94 \pm 0.028
	1999	0.0021	0.0000	131.26	0.0000	0.98 \pm 0.011
c_1	1998	0.0005	0.0001	4.45	0.0254	0.57 \pm 0.145
	1999	0.0026	0.0002	12.11	0.0000	0.80 \pm 0.082
c_2	1998	0.0017	0.0003	6.00	0.0100	0.61 \pm 0.137
	1999	0.0070	0.0001	57.47	0.0000	0.96 \pm 0.019
c_3	1998	0.0090	0.0021	4.70	0.0216	0.55 \pm 0.149
	1999	0.0059	0.0020	2.92	0.0472	0.39 \pm 0.171

$p < 0.001$; for 1998 and 1999, respectively), the differently measured ES values do not differ significantly ($t = -0.28$, $df = 67$, $p = 0.781$; $t = -0.53$, $df = 44$, $p = 0.598$; for 1998 and 1999, respectively) suggesting that we measured the same shape in both ways despite of the discrepancies between the two sets of length and breadth data. Discrepancies result from our photographing method. During the process the scale was placed on the platform holding the eggs, i.e. the equatorial plan of the eggs and the plane of the scale were not exactly at the same distance from the camera. To support this argument, differences between the two length and breadth data of the eggs were correlated positively to lengths and breadths measured from photos, respectively (for lengths vs differences between lengths: $r_s = 0.3969$, $n = 68$, $p < 0.001$; $r_s = 0.1743$, $n = 45$, $p = 0.126$; for breadths vs differences between breadths: $r_s = 0.3921$, $n = 68$, $p < 0.001$; $r_s = 0.4447$, $n = 45$, $p = 0.001$ in 1998 and 1999, respectively). These results suggest that our photographing method does not distort the shape of eggs, i.e. it may be suitable to examine egg shape.

Mean values of length, breadth, ES , c_0 , c_1 , c_2 and c_3 for each female and for the studied population are shown in Table 2. Repeatabilities calculated from one-way ANOVAs ranged from 0.65 to 0.92, calculated from nested ANOVAs ranged from 0.21 to 0.60 for c_1 , c_2 and c_3 . In the case of length, breadth, ES and c_0 repeatability values were not significant (Table 3–4). All repeatability values calculated from nested ANOVAs were lower than the corresponding ones calculated from one-way ANOVAs, except of repeatability for length in 1999.

The similar results for ES and c_0 are not surprising because ES is the length divided by the maximal breadth (B_{max}), c_0 is the length divided by equatorial breadth (B_{eq}) and in the case of most avian egg there is a very little difference between B_{max} and B_{eq} (PRESTON 1974). Accordingly, these two parameters correlate

Table 2. Mean values and SD of egg shape parameters (c_0 , c_1 , c_2 , c_3 and ES) and size measurements (length, breadth) for each female in the studied Tree Sparrow population. Number of measured eggs (n) is shown in parentheses after each female identification number

female	(n)	c_0		c_1		c_2		c_3		ES		length		breadth	
		mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
1998															
98.1	(10)	0.752	0.031	-0.041	0.027	-0.015	0.026	0.013	0.026	0.752	0.031	18.59	0.680	13.98	0.615
98.2	(12)	0.722	0.019	-0.105	0.022	-0.012	0.029	-0.037	0.041	0.729	0.021	19.77	0.911	14.40	0.435
98.3	(15)	0.714	0.049	-0.101	0.015	0.022	0.024	-0.053	0.042	0.721	0.049	19.65	0.968	14.13	0.457
98.4	(4)	0.708	0.010	-0.105	0.029	-0.011	0.029	-0.049	0.036	0.714	0.011	20.37	0.250	14.55	0.216
98.5	(8)	0.718	0.017	-0.109	0.021	-0.022	0.023	-0.038	0.037	0.725	0.017	19.18	0.375	13.92	0.316
98.6	(9)	0.700	0.033	-0.120	0.021	-0.003	0.027	-0.076	0.051	0.707	0.032	20.63	0.613	14.58	0.319
98.7	(6)	0.703	0.021	-0.122	0.011	-0.012	0.035	0.000	0.045	0.709	0.018	21.00	0.414	14.89	0.222
98.8	(4)	0.721	0.025	-0.075	0.017	-0.001	0.037	0.013	0.023	0.724	0.025	20.03	0.663	14.50	0.122
all	(68)	0.719	0.034	-0.097	0.032	-0.004	0.030	-0.033	0.048	0.724	0.033	19.77	1.002	14.30	0.492
1999															
99.1	(15)	0.727	0.019	-0.053	0.027	-0.032	0.021	-0.065	0.068	0.729	0.036	20.09	0.753	14.65	0.349
99.2	(4)	0.705	0.032	-0.135	0.023	-0.003	0.022	0.045	0.028	0.715	0.063	20.38	0.815	14.57	0.105
99.3	(16)	0.698	0.019	-0.101	0.015	0.008	0.027	0.007	0.058	0.705	0.038	20.89	0.602	14.74	0.497
99.4	(10)	0.743	0.040	-0.079	0.042	-0.029	0.026	-0.079	0.121	0.747	0.068	20.04	0.847	14.98	0.386
all	(45)	0.718	0.031	-0.083	0.037	-0.014	0.030	-0.032	0.087	0.723	0.055	20.39	0.802	14.75	0.416

Table 3. Results of one-way ANOVAs and repeatabilities (r) of clutch means of egg traits of Tree Sparrow females in 1998 and 1999

parameter	years			
	1998 (df = 7 and 7)		1999 (df = 3 and 5)	
	F value ^(a)	$r \pm SE$	F value ^(a)	$r \pm SE$
length	2.1962 ^(NS)	0.36 \pm 0.154	1.0579 ^(NS)	0.03 \pm 0.158
breadth	1.1760 ^(NS)	0.08 \pm 0.182	0.3366 ^(NS)	NA ^b
<i>ES</i>	0.4238 ^(NS)	NA ^b	2.1920 ^(NS)	0.42 \pm 0.136
c_0	0.5536 ^(NS)	NA ^b	2.4596 ^(NS)	0.47 \pm 0.129
c_1	11.5786 ^(**)	0.84 \pm 0.050	26.4543 ^(**)	0.92 \pm 0.026
c_2	3.7210 ^(*)	0.65 \pm 0.100	12.3403 ^(**)	0.85 \pm 0.047
c_3	6.8566 ^(**)	0.70 \pm 0.088	6.5465 ^(*)	0.76 \pm 0.071

^a significance levels (NS: not significant, $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$)

^b NA: repeatability is not applicable because F-value is smaller than 1

strongly ($r_s = 0.9887$, $n = 113$, $p < 0.001$) and can be considered as equivalent egg shape specifiers. Using c_1 , c_2 and c_3 additional parameters provides more information on egg shape than *ES* alone. Furthermore, results of analyses of variance show that these parameters are sufficiently sensitive to yield significant differences even with our small sample size. This may be due to that these additional shape-specifiers are much more variable than breadth, length and *ES*. In the studied population ($n = 113$; eggs pooled for the two years) the coefficients of variation for breadth, length, *ES* and c_0 ranged from 3.53% to 4.86%, while for c_1 , c_2 and c_3 its were 38.18%, 365.18% and 1063.31%, respectively.

Table 4. Among females repeatabilities (r) of egg traits of Tree Sparrow females in 1998 and 1999 from nested ANOVAs, clutches are grouped within particular females

parameter	years			
	1998 (df = 7 and 7)		1999 (df = 3 and 5)	
	F value ^(a)	$r \pm SE$	F value ^(a)	$r \pm SE$
length	2.2613 ^(NS)	0.31 \pm 0.141	1.1218 ^(NS)	0.05 \pm 0.116
breadth	1.1819 ^(NS)	0.06 \pm 0.084	0.2978 ^(NS)	NA ^b
<i>ES</i>	0.4013 ^(NS)	NA ^b	2.2156 ^(NS)	0.23 \pm 0.205
c_0	0.5444 ^(NS)	NA ^b	2.5783 ^(NS)	0.28 \pm 0.222
c_1	13.0899 ^(**)	0.60 \pm 0.134	23.2565 ^(*)	0.54 \pm 0.237
c_2	3.6932 ^(*)	0.21 \pm 0.126	12.0386 ^(*)	0.43 \pm 0.244
c_3	7.0572 ^(**)	0.37 \pm 0.146	5.7153 ^(NS-)	0.29 \pm 0.223

^asignificance levels (NS: not significant, $p > 0.05$; ~: $p < 0.10$; *: $p < 0.05$; **: $p < 0.01$)

^bNA: repeatability is not applicable because F-value is smaller than 1

DISCUSSION

In this study we were interested to estimate repeatability values of some well-elaborated egg shape parameters of Tree Sparrow eggs. Nested ANOVAs (FLINT *et al.* 2001) resulted in moderate repeatability estimates (ranges 0.21–0.60) for c_1 , c_2 and c_3 egg shape parameters and much higher repeatability values (ranges 0.65–0.92) derived from the corresponding one-way ANOVAs. Repeatability estimates of egg shape traits using one-way and nested ANOVA differ similarly as it was found in a previous work (for *ES* in BANBURA & ZIELINSKY 1998) and support FLINT *et al.* (2001) results, i.e. the true repeatability value of egg traits should be calculated using hierarchical variance analysis. A simple (not hierarchical) one-way ANOVA cannot take account both within-female among clutches and within-female within clutches variability and so thus may seriously overestimate the true value of among female repeatability. In case of c_1 , c_2 and c_3 shape-specifiers we detected significantly greater among- than within-female variance which may occur due to heritable genetic variance, maternal effects or interaction of genetic and environmental factors (FALCONER 1989, RIDLEY 1993).

As, we were not able to check (e.g. by DNA fingerprinting) the genetic mother of the eggs, our repeatability calculations are based on clutches which may contain eggs laid by conspecifics. This phenomenon, which is called intraspecific brood parasitism or egg dumping, can be considered as a source of error in our repeatability analyses. Egg dumping increases the within clutch variance, i.e. in the case of nested ANOVA based estimates it decreases, in the case of one-way ANOVA based estimates it increase our estimated values. As intraspecific brood parasitism usually has a very low frequency (MØLLER & BIRKHEAD 1993, PERREAU *et al.* 1997) so the caused error may be of little amount. CORDERO *et al.* (2002) analysed the DNA profile of hatched nestlings of 75 broods of Tree Sparrow and found any offspring denoting to egg dumping (PHILIPP HEEB pers. comm.). However, the last egg of a Tree Sparrow brood often differs from earlier ones in size, shape and colour (SUMMER-SMITH 1995, pers. observations) and it may have similar effect on our repeatability estimates than an incidental egg dumping, since we assume that the true repeatability of the studied parameters may located between values estimated by the means of the two way of repeatability calculations.

Repeatability of *ES* has been investigated in numerous avian groups, i.e. geese (BATT & PRINCE 1978, DUNCAN 1987, LEBLANC 1989), shorebirds (THOMAS *et al.* 1989), and passerines (VAN NOORDWIJK *et al.* 1981, HENDRICKS 1991, HORAK *et al.* 1995) and these authors found high repeatability values for *ES*. We found c_1 , c_2 and c_3 are more variable among females, while *ES* which is derived from length

and breadth, and the related c_0 have more variation within females. Hence, in Tree Sparrows we found egg shape to be more repeatable than egg size, similarly to the results of PETERSEN (1992) in the case of Emperor Geese. Egg size (length, breadth) and egg size dependent parameters (ES , c_0) may be influenced considerably by environmental factors (BANBURA & ZIELINSKY 1998), including quality (KRAPU 1979, DUNCAN 1987, PEHRSSON 1991), and abundance of food (NILSSON & SVENSSON 1993), daily surplus of energy and nutrients (PERRINS 1996), and the condition of the female (SMITH *et al.* 1993). In contrast, parameters not so sensitive to egg size variation like c_1 , c_2 and c_3 were more consistent in this study and may more likely be influenced by genetic factors.

The described method detects small differences among egg shapes, suggesting that it may be useful to study intraspecific brood parasitism. A paper on intraspecific brood parasitism (PETERSEN 1992) used parameters calculated from distances of specific points of eggs. We suggest that our method which is based on describing the outline of eggs with a function, may give a better chance to identify parasite eggs. BAKER (2002) recently published a simple analytic method to describe egg shape using two parameters: elongation and asymmetry. He tested his method on the eggs of 250 bird species, however, he used one egg of each species in his analyses, since he did not investigate intraspecific variability of egg shape. To make sure of which method is more suitable to study intraspecific egg shape variability the two methods must be compared in the future.

The mentioned function is also suitable to calculate egg volume. Integrating equation 3 from $-a$ to a gives the volume of the egg. So, photographing eggs and finding the best fitting function parameters allow us to simply estimate egg volume. This kind of egg volume estimation does not ignore egg shape variation (as authors often do it: HENDRICKS 1991, BANBURA & ZIELINSKY 1998, AMAT *et al.* 2001), which may be important when someone is interested to measure exact volume of individual eggs.

*

Acknowledgements – We are grateful to K. PECSENYE for providing access to an image processing system, J. SERFÓZÓ and J. L. SZENTPÉTERI for their valuable help in fieldwork, K. BERTÓK for helping us in some mathematical problems, J. M. C. HUTCHINSON, G. KARDOS, P. L. FLINT and two anonymous referees for their comments on earlier drafts of this paper. This study was partly supported by an OTKA (Hungary) GRANT # T030434 to ZB. ZB was supported by a János Bolyai Research Fellowship and a György Békéssy Postdoctoral Fellowship.

REFERENCES

- AMAT, J. A., FRAGA, R. M. & ARROYO, G. O. (2001) Intraclutch egg-size variation and offspring survival in the Kentish Plover *Charadrius alexandrinus*. *Ibis* **143**: 17–23.
- ANDERSSON, M. (1978) Optimal eggshape in waders. *Ornis Fenn.* **55**: 105–109.
- AR, A., PAGANELLI, C. V., REEVES, R. B., GREENE, D. G. & RAHN, H. (1974) The avian egg: Water vapour conductance, shell thickness and functional pore area. *Condor* **76**: 153–158.
- BAIN, M. M. (1991) A reinterpretation of egg shell strength. Pp. 131–145. In SOLOMON, S. E. (ed.): *Egg and eggshell quality*. Wolfe Publishing Limited, Aylesbury.
- BAIN, M. M. & SOLOMON, S. E. (1991) Cracking the secret of eggshells. *New Sci.* **129**: 27–29.
- BAKER, D. E. (2002) A geometric method for determining shape of bird eggs. *Auk* **119**(4): 1179–1186.
- BANBURA, J. & ZIELINSKY, P. (1998) An analysis of egg-size repeatability in barn swallows *Hirundo rustica*. *Ardeola* **45**(2): 183–192.
- BARTA, Z. & SZÉKELY, T. (1997) The optimal shape of avian eggs. *Funct. Ecol.* **11**: 656–662.
- BATT, B. D. & PRINCE, H. H. (1978) Some reproductive parameters of Mallards in relation to age, captivity, and geographic origin. *J. Wildl. Manage.* **42**: 834–842.
- BECKER, W. A. (1984) *Manual of quantitative genetics*. Academic Enterprises. Pullman, Washington.
- BOZSKO, SZ. I. (1968) Ornithological observations in the Botanical Garden of Kossuth Lajos University of Debrecen in the summer of 1967. *Acta Biol. Debr.* **6**: 5–22. [in Hungarian]
- BOZSKO, SZ. I. & PAPP, L. (1980) Changes in the ornithofauna of the Botanical Garden of Debrecen from 1967 to 1980. *Acta Biol. Debr.* **17**: 205–214. [in Hungarian]
- BROWN, C. R. & SHERMAN, L. C. (1989) Variation in the appearance of swallow eggs and the detection of intraspecific brood parasitism. *Condor* **91**: 620–627.
- CARTER, T. C. & JONES, R. M. (1970) The hen's egg: Shell shape and size parameters and their interrelations. *Br. Poult. Sci.* **11**: 179–188.
- CORDERO, P. J., HEEB, P., WETTON, J. H. & PARKIN, D. T. (2002) Extra-pair fertilizations in Tree Sparrows *Passer montanus*. *Ibis* **144**: E67–E72.
- DRENT, R. (1975) Incubation. Pp. 333–420. In FARNER, D. S., KING, J. R. & PARKES, K. C. (eds): *Avian biology*, Vol. 5. Academic Press, New York.
- DUNCAN, D. C. (1987) Variation and heritability in egg size of the Northern Pintail. *Can. J. Zool.* **65**: 992–996.
- ERŐSS, L. (1983) The function of shape in bird's eggs. *Aquila* **90**: 159–175.
- FALCONER, D. S. (1989) *Introduction to quantitative genetics*. Longmann, Harlow.
- FLINT, P. L., ROCKWELL, R. F. & SEDINGER, J. S. (2001) Estimating repeatability of egg size. *Auk* **118**: 500–503.
- GRANT, P. R. (1982) Variation in the size and shape of Darwin's finch eggs. *Auk* **99**: 15–23.
- HENDRICKS, P. (1991) Repeatability of size and shape of American Pipit eggs. *Can. J. Zool.* **69**: 2624–2628.
- HICKS, A. F., JR. (1958) Heritability and correlation analysis of egg weight, eggshape and egg number in chickens. *Poultry Sci.* **38**: 967–975.
- HORAK, P., MÄND, R., OTS, I. & LEIVITS, A. (1995) Egg size in the Great Tit *Parus major*: individual, habitat and geographic differences. *Ornis Fenn.* **72**: 97–114.
- KRAPU, G. L. (1979) Nutrition of female dabbling ducks during reproduction. Pp. 59–70. In BOOKHOUT, T. A. (ed.): *Waterfowl and wetlands – an integrated review*. Proc. 1977 Symp. Madison, WI, NC Sect, The Wildlife Society. La Crosse Printing Co., La Crosse, Wisconsin.

- LEBLANC, Y. (1989) Variation of size of eggs of captive and wild Canada Geese. *Ornis Scand.* **20**: 93–98.
- LESSELS, C. M. & BOAG, P. T. (1987) Unrepeatable repeatabilities: A common mistake. *Auk* **104**: 116–121.
- MÄND, R., NIGUL, A. & SEIN, E. (1986) Oomorphology: a new method. *Auk* **103**: 613–617.
- MØLLER, A. P. & BIRKHEAD, T. R. (1993) Certainty of paternity covaries with paternal care in birds. *Behav. Ecol. Sociobiol.* **33**: 261–268.
- MOSKÁT, C., SZENTPÉTERI, J. & BARTA, Z. (2002) Adaptations by great reed warblers brood parasitism: a comparison of populations in sympatry and allopatry with the common cuckoo. *Behaviour* **139**: 1313–1329.
- NILSSON, J. A. & SVENSSON, E. (1993) Energy constraints and ultimate decision during egg-laying in the Blue Tit. *Ecology* **74**: 244–251.
- VAN NOORDWIJK, A. J., KEIZER, L. C. P., VAN BALEN, J. H. & SCHARLOO, W. (1981) Genetic variation in egg dimensions in natural populations of the Great Tit. *Genetica* **55**: 221–232.
- OIEN, I. J., MOKSNES, A. & ROSKAFT, E. (1995) Evolution of variation in egg color and marking pattern in European passerines – adaptations in a coevolutionary arms-race with the cuckoo, *Cuculus canorus*. *Behav. Ecol.* **6**(2): 166–174.
- OLSEN, P. D., CUNNINGHAM, R. B. & DONNELLY, C. F. (1994) Avian egg morphometrics: Allometric models of egg volume, clutch volume and shape. *Aust. J. Zool.* **42**: 307–321.
- PEHRSSON, O. (1991) Egg and clutch size in the Mallard as related to food quality. *Can. J. Zool.* **69**: 156–162.
- PERREAULT, S., LEMON, R. E. & KUHNLEIN, U. (1997) Patterns and correlates of extrapair paternity in American redstarts (*Setophaga ruticilla*). *Behav. Ecol.* **8**: 612–621.
- PERRINS, C. M. (1996) Eggs, egg formation and the timing of breeding. *Ibis* **138**: 2–15.
- PETERSEN, M. R. (1992) Intraspecific variation in eggshape among individual Emperor Geese. *J. Field Ornithol.* **63**(3): 344–354.
- PRESS, W. H., TENKOLSKY, S. A., VETTERLING, W. T. & FLANNERY, B. P. (1992) *Numerical recipes in C*. 2nd ed. Cambridge University Press.
- PRESTON, F. W. (1953) The shapes of birds' eggs. *Auk* **70**: 160–182.
- PRESTON, F. W. (1968) The shapes of birds' eggs: mathematical aspects. *Auk* **85**: 454–463.
- PRESTON, F. W. (1969) The shapes of birds' eggs: extant north american families. *Auk* **86**: 246–264.
- PRESTON, F. W. (1974) The volume of an egg. *Auk* **91**: 132–138.
- RIDLEY, M. (1993) *Evolution*. Blackwell Science, Boston.
- SMITH, H. G., OTTOSSON, U. & OHLSSON, T. (1993) Interclutch variation in egg mass among Starlings *Sturnus vulgaris* reflects female condition. *Ornis Scand.* **24**: 311–316.
- STOKKE, B. G., MOKSNES, A. & ROSKAFT, E. (2002) Obligate brood parasites as selective agents for evolution of egg appearance in passerine birds. *Evolution* **56**(1): 199–205.
- SUMMERS-SMITH, J. D. (1995) *The Tree Sparrow*. Published by J. D. Summers-Smith.
- THOMAS, C. J., THOMPSON, D. B. A. & GALBRAITH, H. (1989) Physiognomic of variation in Dotterel *Charadrius morinellus* clutches. *Ornis Scand.* **20**: 145–150.
- TODD, P. H. & SMART, I. H. M. (1984) The shape of birds' eggs. *J. Theor. Biol.* **106**: 239–243.
- TSERVENI-GOUSHI, A. S. & YANNAKOPOULOS, A. L. (1995) Effect of age at sexual maturity on egg-shape in pullets during the early laying period. *Poultry Sci.* **74**: 279–284.
- WILLIAMS, T. D. (1994) Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. *Biol. rev. Camb. Philos. Soc.* **68**: 35–59.

Revised version received March 24, 2005, accepted May 23, 2005, published June 30, 2005