Zoological Studies **57:** 2 (2018)
doi:10.6620/ZS.2018.57-02

Zoological Studies

Open Access

Weather Conditions Influence Egg Volume Repeatability in Clutches of the Red-backed Shrike *Lanius collurio*

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(Received 6 December 2016; Accepted 29 December 2017; Published 25 January 2018; Communicated by Chih-Ming Hung)

Citation: Golawski A, Mitrus C. 2018. Weather conditions influence egg volume repeatability in clutches of the Red-backed Shrike *Lanius collurio*. Zool Stud **57:**2. doi:10.6620/ZS.2018.57-02.

Artur Golawski and Cezary Mitrus (2018) Birds show considerable variation in egg size, both within and between clutches. There are many factors affecting egg dimensions including features of the birds themselves, territory quality, food abundance and weather conditions. One feature that varies in clutches is repeatability of egg dimensions within a clutch. We studied variation in egg size in clutches of the Red-backed Shrike *Lanius collurio* in east-central Poland and examined the effects of territory quality and weather conditions on egg size repeatability. Repeatability of egg size was low and ranged from 0.51 to 0.55. No significant differences in egg dimensions were found between clutch size classes (3 to 7 eggs, modal clutch size of 6). Weather conditions only influenced repeatability of egg volume. This parameter was affected by the year and one environmental factor - total rainfall immediately before egg laying. With increasing rainfall, the repeatability of egg volume decreased. Weather conditions can influence food availability and in this way also affect egg size. The Red-backed Shrike diet consists mainly of insects, the activity of which significantly decreased during rainfall. In such conditions, birds have to spend more energy to gain food, which could consequently lead to differences in egg size.

Key words: Egg dimensions, Farmland, Repeatability, Rainfall, Territory quality, Weather.

BACKGROUND

Birds show considerable variation in egg size within a clutch and it is known that egg size can influence the reproductive output of birds, especially by affecting the growth (Järvinen and Ylimaunu 1986) or survival rates of nestlings (Williams 1994). For many birds - including Passerines - daily nutrient intake affects egg production (Perrins 1996; Ward and Bryant 2006). As a consequence, nutrient availability is likely to set a constraint on egg size by influencing the process of egg formation (Martin 1987). Environmental stress on individuals can also influence egg size, *e.g.* changes in food availability (Bańbura and Zieliński 1998; Christians 2002). Evidence also exists that animals have been affected by weather conditions and recent climate change (Tryjanowski et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). These affects have led to changes in population sizes and densities and their distributions, timing of migration and changes in breeding performance - including egg size (Crick 2004; Walther et al. 2017). One major concern is that climate change will lead to more extreme weather events (Easterling et al. 2000) and have a significant influence on the breeding biology of birds, including, for example, an increase

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in egg size variation within clutches.

In addition to variation in weather conditions, territory structure and quality can strongly affect food abundance (Golawski and Meissner 2008) and thus also environmental stress on individuals. It has been shown that territory quality can significantly influence egg size (Parker and Begon 1986; Bańbura et al. 2010), such that a higher food availability was related to reduced variation in egg volume (Takagi 2003). Recently, substantial changes in farmlands - including the disappearance of marginal habitats rich in biodiversity - have been observed (Büchs 2003; Brambilla et al. 2010); this has the potential to also negatively affect birds (Evans 2004; Tryjanowski et al. 2011; Morelli 2013). As a consequence, it is expected that birds' egg sizes differ between habitats with different food supplies (Chabi et al. 2000; Bourgault et al. 2007).

These two factors - weather conditions and territory quality - can influence environmental stress on individuals and thus on egg size. A relatively easy way to effectively evaluate the impact of environmental conditions on egg dimensions is to estimate repeatability of egg parameters in clutches (Bańbura and Zieliński 1990; Falconer and Mackay 1995). Variation in egg dimensions results from both genetic determination and the impact of environmental conditions. High repeatability suggests that phenotypic variance has a significant heritable component and low repeatability suggests a significant environmental component (Bańbura and Zieliński 1998).

The main goal of this study was to examine how susceptible variation in egg dimensions is to environmental influences in female Red-backed Shrikes *Lanius collurio* breeding in farmland in east-central Poland. We wanted to examine which had the stronger effect on egg size repeatability: territory quality or weather conditions at egg laying time.

MATERIALS AND METHODS

Study area

The study was carried out in east-central Poland, near Siedlce (52°12'N, 22°17'E) from 2000-2002. The study area consisted of 855 ha of extensive agricultural landscape. Arable fields predominated in this area (53.5%), mainly with rye and potato crops. Meadows and pastures covered 21.1% and the proportion of set-asides was 2.2%. Woodlands and apple orchards were also present in addition to these open habitats. Red-backed Shrikes occupied open habitats at the edges of woodlands, orchards or scattered trees and bushes.

Bird data

The Red-backed Shrike is widespread in Europe with stabilised population estimates ranging from 6,300 to 13,000 million breeding pairs (BirdLife International 2004). Breeding occurs in various habitats, such as woodland edges, forest plantations and orchards. However, the largest numbers of breeding pairs occur in farmland (Cramp and Perrins 1993). The average density of the Red-backed Shrike in the study area in this period was 0.6 pair/10 ha (Goławski 2006). Very low philopatry was observed in the local population (Tryjanowski et al. 2007).

We looked for Red-backed Shrike nests between mid-May and the end of July from 2000-2002, checking all possible locations favorable for nesting. Nests were checked only 2-3 times due to the possibly strong human impact on nest success (Tryjanowski and Kuźniak 1999). We measured eggs only in completed clutches (N = 75) at the end of the incubation period. The maximum length and breadth were measured with sliding calipers to the nearest 0.1mm. All eggs were measured by one person (AG), which eliminated any inter-observer variability. We calculated the egg volume index (V) from the length (L) and breadth (B) using the formula re-scaled for Red-backed Shrike: $V = 0.5322 \times L \times B^2$ (Surmacki et al. 2006). Repeatability of egg size within clutches was calculated as the intra-class correlation coefficient using variance components derived from one-way ANOVA and following Lessells and Boag (1987), by applying the formula: $r = (MS_A - MS_W)/[MS_A + (n_0 - 1) MS_W]$, where MS_A is the between-clutch mean square, MS_W is the within-clutch mean square and n_0 is a coefficient related to sample size per group in ANOVA, given by: $n_0 = 1/(a - 1) * [\Sigma n_i (\Sigma n_i^2/\Sigma n_i)]$, where ni is the size in the i-th group and a is the number of groups (Lessells and Boag 1987). Mean values for all egg characteristics in each clutch were used as unit observations throughout this paper to avoid pseudoreplication (Lessells and Boag 1987).

Habitat structure in territories

The average territory size for this species is 1.5 ha, based on studies of its biology and breeding ecology conducted throughout many countries in Europe (Cramp and Perrins 1993). Thus, the present study utilized this territory size using the method described below and previously used by Golawski and Meissner (2008). Around each nest, a hypothetical territory 70 m in radius was drawn and a circle of 1.54 ha area was obtained. Because the Red-backed Shrike does not use the insides of woodlands, established territories that included woodlands were limited to a 7 m wide strip of the woodland edge (the greatest distance from the woodland edge in which a nest was found). Other habitat components were included in these territories and their radii were enlarged to obtain a territory size equal to 1.54 ha. The territory structures are presented in table 1. Having one person (AG) describe territories guaranteed the same precision in drawing sketches of the territory characteristics.

Weather data

Weather data were obtained from the website: http://www.tutiempo.net for the nearest meteorological station in Siedlce town (10 km south of the study area). We assumed, after Diehl's study (1998), that the size of eggs in the clutch might be affected by the weather of the week starting 4 days before the laying date of the first egg. As well as weekly average temperature, total rainfall (in mm) in this period was also taken into account. These two weather factors were used in other papers to ask questions similar to ours (*e.g.* Górski et al. 2015; Parejo et al. 2015).

Statistical analysis

We analysed the influence of average temperature, amount of rainfall and structure of habitats in each territory on the repeatability of egg parameters in the Red-backed Shrike. A principal components analysis (PCA) was carried out with habitat variables describing the 75 territories to obtain a reduced number of factors that summarized habitat structure. Only PCs with eigenvalues > 1 were retained.

We used generalised linear models to test for the effects of territory habitat structure (four scores of PCA) and weather conditions (average temperature and total rainfall) on the repeatability of egg parameters in the Red-backed Shrike. In single GLM with 7 covariates we included three egg parameters - length, breadth and volume - and did three separate analyses. In the calculation, the year was added as a categorical factor. The rest of the variables were treated as continuous predictors. Values describing egg repeatability matched Gaussian distributions. Variables describing weather data were square root transformed. To test for the presence of a trade-off between egg size and clutch size, we also used GLM (normal distribution of all dependent variables), and in analyses the year was added as a categorical factor and the average temperature and total rainfall as a continuous predictors. The level of statistical significance was set at a = 0.05 in all analyses. We used Statistica 10.0 (StatSoft

Table 1. Territory structure and principal components analyses performed with 11 variables defining habitat structure in 75 territories of Red-backed Shrikes. Significant correlations between original variables and components (all $P < 0.01$) are shown in bold

Variable	Mean	Range	PC1	PC2	PC3	PC4
Fences (m)	34.7	0-231	**-0.80**	-0.23	0.03	0.03
Ditches (m)	49.8	0-282	**-0.60**	-0.21	0.06	-0.12
Roads (m)	67.7	0-230	0.19	**-0.70**	0.10	**-0.32**
Hedges (m)	56.4	0-274	**-0.78**	**-0.42**	-0.10	0.03
Meadows (ha)	0.53	0-1.54	**-0.52**	**0.68**	**0.33**	-0.15
Pastures (ha)	0.16	0-1.44	**-0.49**	-0.25	**-0.51**	-0.25
Fallows (ha)	0.13	0-1.07	0.15	**-0.46**	**0.43**	**0.37**
Fields (ha)	0.41	0-1.53	**0.73**	-0.19	-0.22	**-0.52**
Orchards (ha)	0.21	0-1.54	0.16	-0.13	-0.12	**0.86**
Settlements (ha)	0.01	0-0.33	0.08	**-0.40**	**0.63**	-0.06
Trees (no.)	0.7	0-6	-0.08	0.12	**0.71**	-0.24
Eigenvalue	-	-	2.74	1.73	1.52	1.42
% variance accounted for	-	-	0.25	0.16	0.14	0.13

2011) software for statistical calculations.

RESULTS

Red-backed shrike clutches (*n* = 75) contained 3 to 7 eggs. Mean clutch size was 5.3 ± 0.81 (mean ± SD) and modal clutch size was 6 eggs. The mean egg length was 22.07 ± 0.83 mm, breadth 16.51 ± 0.41 mm and volume 3.21 ± 0.22 cm^3. Egg dimensions were similar for all 3 breeding seasons (Table 2).

No significant differences in egg dimensions were found between clutch size classes; other variables included in the model were year, mean temperature, and total rainfall no influenced on egg dimensions ($GLM_{egg\ length}$ = 1.17, p = 0.330; $GLM_{egg\ breadth}$ = 0.64; p = 0.738; $GLM_{egg\ volume}$ = 0.95, p = 0.483, respectively). Repeatability estimates were low and ranged from 0.51 to 0.55 (Table 3).

The four principal components (PC1- PC4) accounted for 68% of the total variation in the habitat structure of territories, with eigenvalues > 1. PC1 accounts for 25% of original variance. Fence and hedge length showed the highest negative correlation with PC1 scores. Meadow area (positive) and road length (negative) provided the major loading on PC2 (16% of original variance). Settlement area and number of single trees showed a positive correlation with PC3 (14% of original variance). And lastly, orchard area showed the highest positive correlation with PC4 score (13% of original variance, Table 1).

Generalised linear models of habitat territory structures (PC1-PC4) and weather conditions on the repeatability of egg dimensions showed statistical significance only in the case of egg volume (Table 4). The repeatability of egg volume was affected by year and one environmental factor - total rainfall. The repeatability of egg volume decreased with increasing rainfall, but this relationship was weak. Differences in egg volume repeatability between years were also slight, the highest value was 0.6 (in 2001) and lowest was 0.5 (in 2000). The territories' habitat structures (for PC1-PC4) did not significantly influence the repeatability of egg dimensions (Table 4).

DISCUSSION

The mean clutch size of the Red-backed Shrike recorded in this study did not deviate substantially from values found in other European populations (Antczak et al. 2009; Söderström and Karlsson 2011). In this study, we tested the influence of weather conditions and territories' habitat structure on the diversity of egg dimensions in Red-backed Shrike clutches. Repeatability of egg size could be related to the repeatability of environmental stress on laying females (Bańbura and Zieliński 1998; Christians 2002). Overall, the results indicated that weather was a more important factor than habitat structure in the territories for the repeatability of eggs. Among weather factors, only the rainfall in the period before egg laying significantly influenced the repeatability of egg dimensions (egg volume). We did not find relationships between the repeatability of length or breadth of eggs in the clutch. These

Table 2. Egg dimensions (mean ± SD), ambient temperature and total rainfall during the Red-beaked Shrike's 3 month breeding season

Year	Egg length (mm)	Egg breadth (mm)	Egg volume (cm^3)	Mean daily temperature (°C)	Total rainfall (mm)
2000, *n* = 21	22.07 ± 0.87	16.52 ± 0.39	3.21 ± 0.23	16.1	214.4
2001, *n* = 29	22.26 ± 0.77	16.60 ± 0.44	3.27 ± 0.20	16.4	167.9
2002, *n* = 25	21.84 ± 0.84	16.40 ± 0.39	3.13 ± 0.21	18.5	208.8

Table 3. Repeatability values (r) and confidence limits (95% CI) for egg dimensions in a Red-backed Shrike population, *n* = 75 clutches. All *F*-ratios (one-way ANOVA) are significant at $P < 0.050$

Parameter	r	*F*-ratio	95% CI
Length	0.53	2.70	0.48-0.59
Breadth	0.51	4.34	0.46-0.56
Volume	0.55	3.86	0.49-0.60

results indicated that most of the environmental factors studied had no effect on repeatability of egg dimensions in clutches of the Red-backed Shrike in east-central Poland, which is consistent with an earlier study related to clutch size (Golawski 2008).

Values of the repeatability of egg size varied between 0.51 and 0.55 and were low compared with other species; for example, values in a study by Christians (2002) were usually higher than 0.68. Within passerines, similarly low values for the repeatability of egg dimensions are uncommon; however, low values have been noted in Bearded Tits *Panurus biarmicus* (Surmacki et al. 2003) and a small population of Blue Tits *Cyanistes caeruleus* in Algeria (Chabi et al. 2000). Other studies on Red-backed Shrikes from western Poland showed that repeatability of egg volume in the clutch was 0.7 (Tryjanowski et al. 2004). Our results indicate that in east-central Poland, Red-backed Shrike egg dimensions (egg volume) showed low heritability and were mostly determined by environmental conditions. The results' statistical significance for only egg volume was related to the fact that volume increases approximately with the cube of the linear measurements of the egg. However, mechanism of egg production and determination of it's phenotype is not known enough. Similar results were found in the American Pipit *Anthus rubescens* and Bearded Tits (Hendricks 1991, Surmacki et al. 2003, respectively); both studies showed high variability in egg volume. The largest eggs in a population can be two times larger than the smallest ones. The variation in this parameter is probably due be due to the variance accumulation from the computational formulas, which are calculated in such a manner that they inherently contain cumulated variance from the input variables (Bańbura 1996).

Inverterbrate availability - including insects that are food for Red-backed Shrikes (Tryjanowski et al. 2003; Golawski 2006; Morelli et al. 2015) - changes with weather conditions (Cucco and Malacarne 1996; Kuper et al. 2000). Rain and the

Table 4. Generalised linear models of habitat territory structure (PC1-PC4) and weather conditions on repeatability of egg dimensions (length, breadth, volume) in Red-backed Shrikes in east-central Poland

Predictor	Estimate	SE	Wald statistics	*p*-value
		Egg length		
Average temperature	0.34	0.21	2.63	0.105
Sum of rainfall	0.01	0.03	0.15	0.701
PC1	-0.03	0.03	0.62	0.432
PC2	-0.03	0.04	0.49	0.482
PC3	0.01	0.04	0.08	0.779
PC4	-0.01	0.04	0.01	0.923
Year	0.15	0.10	2.21	0.137
		Egg breadth		
Average temperature	0.11	0.20	0.29	0.589
Sum of rainfall	0.04	0.03	2.15	0.140
PC1	0.02	0.03	0.24	0.621
PC2	-0.02	0.04	0.25	0.610
PC3	0.06	0.03	2.86	0.091
PC4	0.06	0.04	2.44	0.118
Year	0.17	0.10	2.55	0.109
		Egg volume		
Average temperature	0.01	0.02	0.01	0.995
Sum of rainfall	**-0.48**	**0.19**	**6.57**	**0.010**
PC1	0.02	0.03	0.58	0.447
PC2	-0.03	0.04	0.73	0.393
PC3	0.03	0.03	0.85	0.357
PC4	0.04	0.04	0.94	0.330
Year	**0.30**	**0.09**	**10.18**	**0.001**

drop in temperature it leads to cause a distinct decrease in the numbers of insects (Grüebler et al. 2008). Furthermore, a large amount of variation in egg size is dependent on a high-quality diet (Williams 1996), which can also be related to weather conditions. Thus, rainfall and a likely decrease in food availability probably influenced egg volume repeatability in the clutch and the low values of repeatability of egg dimensions and was consistent with results from a study on Bearded Tits (Surmacki et al. 2003). In this species, changes in food abundance in the littoral zone of a lake had a significant influence on the repeatability of egg dimensions. If the food supply for laying females varies across short timescales, it can affect their condition and this can influence mean egg size. Thus, potential environmental stress affects female condition and, consequently, repeatability of egg volume (Tryjanowski et al. 2004). Differences in the repeatability of egg volume within the clutch were also observed in relation to the year of study. The highest value was noted in 2001; the 3 months recorded in 2001 (May-July) had much less rainfall (167.9 mm) than the same months in 2000 and 2001 did (214.4 mm and 208.8 mm respectively, Table 2). As well as variation in rainfall, food abundance may also have an influence on results and may also vary year-by-year (Hill 1985).

Habitat structure did not have a significant influence on egg dimension repeatability. Habitat structure within the same sample area did not affect clutch size but did influence the number of fledglings (Golawski and Meissner 2008). Various habitats used by shrikes differed in food abundance (Golawski and Golawska 2008), but weather conditions can have an additional influence on food availability, which may make weather conditions more important (Rodenhouse and Holmes 1992; Tryjanowski et al. 2003).

CONCLUSIONS

For Red-backed Shrikes in east-central Poland, the weather is a more important factor influencing on repeatability of egg dimensions than territory quality. Consequently, in the event of climate change increasing the incidence of extreme rainfall (Sanz 2002), this factor may influence optimal egg size in the future and have effects on the condition, size and dynamics of Red-backed Shrike populations.

Acknowledgments: We thank Shelley Hinsley for providing comments that improved the quality of the manuscript and for correcting the English. We are also grateful to the two anonymous reviewers for their critical remarks regarding the first version of this paper. This study complies with current Polish laws and was financially supported by the Siedlce University of Natural Sciences and Humanities (AG) and the University of Rzeszów (CM).

Authors' contributions: AG and CM performed the field work and written the manuscript. All authors contributed to drafting and revising the manuscript. All authors read and approved the final manuscript.

Competing interests: AG and CM declare that they have no conflict of interests regarding the publication of this paper.

Availability of data and materials: Data and materials are available in Department of Zoology University of Natural Sciences and Humanities in Siedlce.

Consent for publication: Not applicable.

Ethics approval consent to participate: This study complies with current Polish laws.

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