Variation in egg-size traits of the European Roller (*Coracias garrulus*) in eastern Poland

Andrzej Górski, Jacek J. Nowakowski & Jerzy Bańbura*

A. Górski, J.J. Nowakowski, Department of Ecology and Environmental Protection, University of Warmia and Mazury in Olsztyn, Plac Łódzki 3, 10-727 Olsztyn, Poland
*J. Bańbura, Department of Experimental Zoology and Evolutionary Biology, Faculty of Biology and Environmental Protection, University of Łódź, Banacha 12/16, 90-237 Łódź, Poland. * Corresponding author's e-mail: jbanb@biol.uni.lodz.pl*

Life-history theory predicts that allocation of resources into offspring size and number should be traded-off. The trade-off may be masked in good environmental conditions and be expressed only in some reproductive attempts, when conditions are poor. In this paper we analyse variation in size-related traits of eggs in relation to clutch size in a marginal population of the European Roller (*Coracias garrulus*) in eastern Poland, declining as a result of agriculture intensification and habitat loss. Because large-bodied insects that constitute the main kind of food of Rollers are greatly affected by the weather in spring, we assumed that their abundance may differ from year to year in association with differences in weather conditions. We predicted that egg size-clutch size relationship and egg traits should differ between years in correspondence with environmental conditions prior to the time of egg laying. We also predicted that variation in egg size and shape should have some fitness-related consequences. We found that year and clutch size interacted in their influence on egg size: in one year egg size was positively and in another year negatively related to clutch size. We also found that egg shape (sphericity) was positively associated with clutch size and negatively related with the date of laying. Both egg size and sphericity in shape positively affected hatching success, thus confirming the existence of fitness-consequences of variation in the traits of Roller eggs. Our results are in general consistent with theoretical expectations, but we failed to find any specific links between egg size variation and the decline of the study population.

1. Introduction

Offspring sizes and numbers are considered as main life-history traits evolving adaptively under pressures of natural selection (Stearns 1992). Because resources in general and resources necessary to produce eggs in particular are limited, a trade-off between egg size and clutch size is postulated by life-history theory, with females laying either numerous small eggs or less numerous large ones (Smith & Fretwell 1974, Stearns 1992). As larger offspring have higher fitness than smaller offspring, Smith & Fretwell (1974) predicted that females should optimally balance the size and number of eggs. Because it is virtually impossible to manipulate egg sizes in birds, analyses of the egg

size/clutch size trade-off in wild bird populations have been based on phenotypic correlations and produced confusing results. For example, Ojanen *et al.* (1978) found that egg sizes decreased with clutch size in Redstarts (*Phoenicurus phoenicurus*), whereas, on reverse, the correlation was positive in Great Tits (*Parus major*) and Starlings (*Sturnus vulgaris*), with no relation occurring in Pied Flycatchers (*Ficedula hypoleuca*). Such findings seem to result from the fact that laying females differ very much in their individual ability to get resources at the optimal time for breeding (Perrins 1996), so that high-quality females can lay large clutches of large eggs, while low-quality females can only lay small clutches of small eggs (Reznick 1985, Stearns 1992). Järvinen (1996) suggested that another factor that obscure the clutch size/egg size trade-off may result from differences in breeding conditions between years. He found that in Pied Flycatchers the trade-off appeared in cold summers but not in warm summers, which in north Finland corresponds to bad and good breeding conditions, respectively.

The shape of eggs is not usually considered in the context of the egg size-clutch size trade-off, but it was suggested that egg length and breadth may undergo different selection pressures (Chylarecki 1993), leading to different patterns of variation in egg size and shape. A model of optimal shape of eggs offered by Barta & Székely (1997) assumed that egg shape at a given clutch size should maximize the number of eggs simultaneously touching the incubation patch. This could potentially lead to a specific relation between egg shape and clutch size. Besides an influence on the efficiency of incubation, egg shape may also constrain the development of some morphological structures of the embryo, possibly affecting hatching and the early nestling life (Chylarecki 1993). Therefore, studies of egg shapes and their fitness consequences in wild avian populations are worth conducting.

Egg sizes and size-related traits display some consistent patterns of variation: they show characteristic variation between species and races (Väisänen 1969, Makatsch 1976), geographic gradients (Chylarecki *et al.* 1997), differences from year to year (Tryjanowski *et al.* 2004, Skwarska *et al.* 2015) and between habitats (Bańbura *et al.* 2010). Egg traits almost always show low within-

clutch and high among-clutch variation (Bańbura & Zieliński 1990, Christians 2002). In most altricial small and middle-sized birds, eggs are produced from the current resource income which may differ even from day to day, providing a corresponding source of variation in egg sizes (Perrins 1996). Although the biological importance of the patterns of egg size variation still requires additional explanation (Perrins 1996), it has now been confirmed that egg sizes have consequences for fitness (Krist 2011).

In this paper we focus on different aspects of variation in size-related traits of eggs of European Rollers (*Coracias garrulus*) in eastern Poland. The Roller population in Poland has been declining since the start of the twentieth century when the species was still widespread all over the lowland, to 500–600 breeding pairs at the end of the 1980s, and further, to as few as 34 pairs in 2014 (Tomiałojć & Stawarczyk 2003, http://www.monitoringptakow.gios.gov.pl/kraska).   During the period of this study, 1990–1996, the local population in the Kurpie Plain included 30–37 breeding pairs (Górski 2005), with the number being reduced to around 10 pairs at present (own data). Since the 1990s, the Kurpie Plain rollers have constituted a peripheral population at the NW border of the East-European part of the species geographic range. The main reason for this population decline is probably habitat loss and the intensification of agriculture (Górski 2005).

To our knowledge, there are only two papers on egg size variation in the Roller, both concerning Spanish populations (Hellmich 1995, Avilés *et al.* 1999). Some comparative data for Eastern and Central Europe are dispersed in handbooks (Makatsch 1976, Cramp & Simmons 1988), but their statistical value is uncertain because of a lack of information on study procedures.

Intensified agricultural practices negatively influence insect abundance, with the effect being enhanced by disadvantageous weather conditions during spring (Frampton *et al.* 2000, Avilés & Parejo 2004, Parejo *et al.* 2015). Based on life-history theory, we can expect that in poor habitats variation in spring weather conditions may influence reproductive allocation decisions of insectivores, including Rollers, resulting in between-year differences in the egg size-clutch size relationship. Therefore, in this paper we intend to analyse varia-

tion in size and shape of eggs in a declining peripheral population of Rollers and to test if the size and shape of eggs are related to study years, clutch size and the timing of laying. We also expect that variation in egg size and shape should affect fitness. Hence, we examine effects of egg traits on hatching success as a fitness-related indicator.

2. Materials and methods

This study was carried out in 1990–1996 in the area of 492 km^2 of the Kurpie Plain, NE Poland (53°16'19"N; 21°50'17"E). The sculpture of the area was shaped during the last Pleistocene glaciation (the Vistula glaciation) and now it is composed of series of dunes distributed from NW to SE, with peat bogs occurring between them. Altitude ranges from 98 to 144 m a.s.l. Around 40% of the area is covered by fragmented secondary coniferous forests interspersed with pastures, meadows and fields. We used weather data on temperature and rainfall from the Mława station located in the Kurpie Plain deposited in the TuTiempo data base (http://en.tutiempo.net/climate/ws-122700. html). Following Parejo *et al*. (2015) we used mean daily temperature and total rainfall data for 1990-1996 to characterize weather conditions prevailing during one month (16 April–15 May) preceding the start of egg laying in our study population of Rollers.

Field studies were conducted from the end of April through August every year. Based on courtship behaviour of Rollers, occupied breeding territories were recognized and searched in detail for nesting cavities. In most cases Rollers nested in cavities excavated by Green Woodpeckers (*Picus viridis*) and much less frequently by Black Woodpeckers (*Dryocopus martius*). When it was impossible to reach eggs with hand, cavities were inspected with a small mirror fastened to a handle and eggs were collected from and put back into cavities with a spoon-like shrimp-net. A total of 261 eggs in 79 clutches were measured – although the study population was declining, the samples of measured clutches increased from year to year (2 clutches in 1990 and 1991, 10 in 1992, 12 in 1993, 15 in 1994, 17 in 1995, and 21 in 1996). Complete clutches contained 2–5 eggs. Once discovered, the clutches were inspected every 3-5 days. Most nesting cavities were found at the time of egg laying,

which enabled us to estimate the date of clutch onset, but some clutches were found when complete. Because we were able to estimate the laying date to the accuracy of 5 days, the timing of laying was approximated by a five-day-long period (pentad) starting from 1 January.

The length (*L*) and breadth (*B*) of eggs were measured with calipers to the nearest 0.1 mm. Egg volume (*V*) was calculated applying Hoyt's (1979) formula: $V = 0.51 \times L \times B^2$. A shape index of egg sphericity (*S*) was also calculated as the ratio of breadth to length expressed as percentage ($S = 100 \times B / L$), with eggs becoming more spherical when the value of this index inreases. Egg length and breadth were correlated with one another and with both egg volume and shape (correlations of per-clutch mean values ($n = 77$): $r = 0.54$, $p < 0.001$ (*L v. B*); $r = 0.81$, $p < 0.001$ (*L v. V*); $r = –0.65$, $p < 0.001$ (*L v. S*); $r = 0.93$, $p < 0.001$ (*B v. V*); $r = 0.28$, $p = 0.013$ (*B v. S*). Egg volume and shape were not correlated with one another ($r = –0.09$, $p = 0.427$).

Because in virtually all analysed cases avian eggs in individual clutches tend to be non-randomly similar in size and shape to one another (Bańbura & Zieliński 1998, Christians 2002), we started data analyses in this study from calculating overall within-clutch repeatabilities of egg size traits by applying intra-class correlation coefficients (Bańbura & Zieliński 1990, Zar 1996). Standard errors of the repeatabilities were calculated according to Becker (1984).

To analyse inter-annual variation in particular traits of eggs as response variables and to test relationships between the egg traits and clutch size and laying date, we used separate linear mixed models (Heck *et al*. 2010). In these models, year was treated as a fixed factor, clutch ID as a random factor controlling for the non-independence of individual eggs in clutches, and clutch size and laying date (pentad) as covariates. Clutch sizes and laying dates were centered by subtracting grand means from their individual values (Heck *et al*. 2010). The restricted maximum likelihood was used to estimate model parameters, and the Satterthwaite method to approximate degrees of freedom (Heck *et al*. 2010). Full models, including year, clutch size, laying date and their interactions, were simplified stepwise by removing interactions and factors which were non-significant to get final models (Crawley 2003).

Table 1. Grand mean estimates of egg size traits and within-clutch repeatabilities of egg-size traits of Rollers (N = 261 eggs; from 79 clutches).

Egg trait	Mean ± SE	R ± SE	$F_{71,\,182}$	p
Egg length (mm)	35.84 ± 0.15	0.72 ± 0.04	10.11	< 0.0001
Egg breadth (mm)	27.86 ± 0.14	0.75 ± 0.04	11.99	< 0.0001
Egg volume (cm^3)	14.09 ± 0.21	0.81 ± 0.03	16.30	< 0.0001
Egg shape (%)	78.57 ± 0.40	0.51 ± 0.06	4.70	< 0.0001

A generalized linear mixed model was constructed to test for associations between hatching success and per-clutch mean egg volume and egg shape as non-correlated predictors. Because we did not know the hatching status of particular eggs, the number of hatchlings in relation to clutch size in particular broods was treated as hatching success (a binomial dependent variable), with the logit link function being applied (Heck *et al.* 2012). Year was treated as a random factor (to take into account the clustering of the data within years), the estimation of parameters was conducted using the restricted maximum likelihood and the Satterthwaite approximation of degrees of freedom was applied (Heck *et al.* 2012). The non-significant interaction between the predictors was removed to get the final model (Crawley 2003).

All data analyses were conducted using the IBM SPSS Statistics 22 software.

3. Results

Most variation in egg length, breadth, volume and shape of the study population of Rollers was between clutches rather than within clutches, resulting in significant intraclutch repeatabilities (Table 1). In general, differentiation in egg sizes was con-

Table 2. Effects of year, clutch size, laying date and their interactions on egg traits as analysed using four separate linear mixed models, with clutch ID treated as fandom factors; CS – clutch size (mean-centered), LD – laying date (mean-centered). N = 4 eggs (2 clutches) in 1990, 6 (2) in 1991, 25 (10) in 1992, 38 (12) in 1993, 55 (15) in 1994, 66 (17) in 1995 and 67 (21) in 1996.

Y-variable	Effect	Estimate ± SE	F	df	p
Egg length	Year	multiple	1.82	6; 72.1	0.107
	CS	−0.196 ± 0.184	1.13	1; 73.2	0.291
	LD	−0.045 ± 0.099	0.02	1; 69.1	0.651
	Clutch SD	1.445	–	–	–
	Res. SD	0.581	–	–	–
Egg breadth	Year	multiple	0.82	6; 68.5	0.556
	CS	0.079 ± 0.164	3.01	1; 71.6	0.087
	LD	−0.113 ± 0.060	3.57	1; 63.6	0.063
	Year × CS	multiple	2.84	6; 68.4	0.016
	Clutch SD	0.505	–	–	–
	Res. SD	0.214	–	–	–
Egg volume	Year	multiple	1.28	6; 67.8	0.277
	CS	0.087 ± 0.243	1.59	1; 69.9	0.212
	LD	−0.145 ± 0.090	2.58	1; 63.9	0.113
	Year × CS	multiple	3.05	6; 67.7	0.011
	Clutch SD	1.167	–	–	–
	Res. SD	0.356	–	–	–
Egg shape	CS	0.612 ± 0.304	4.05	1; 80.6	0.048
	LD	−0.346 ± 0.149	5.39	1; 73.5	0.023
	Clutch SD	3.848	–	–	–
	Res. SD	4.015	–	–	–

siderable, as shown by a difference between the smallest and the largest individual eggs, 11.09 cm³ and 18.85 cm³, respectively (means of all analysed traits in Table 1).

Analysing linear mixed models for particular egg traits, we found significant effects of interactions between year and clutch size on egg breadth and volume, which means that the effects differ among years (Table 2). The interaction between year and clutch size in the case of egg breadth resulted from a positive relation between this trait and clutch size in 1995 (estimate = 0.962 ± 0.339 SE, $t_{63.3} = 2.83$, $p = 0.006$) and a lack of such a relation in other years. The same was true about egg volume (estimate = 1.348 ± 0.508 SE, $t_{63.7} = 2.65$, $p = 0.01$ in 1995), but in this case a marginally non-significant negative effect occurred also in 1994 (estimate = -0.709 ± 0.372 SE, $t_{67.0} = -1.91$, $p = 0.06$). No effect of year, clutch size, laying date or their interactions on egg length was revealed (Table 2). Moreover, egg shape (sphericity) was positively associated with clutch size and negatively related with the date of laying, with no interaction or year effect occurring in this case (Table 2).

Because egg volume and sphericity are not correlated with one another, we tested for effects of their per-clutch mean values on hatching success and we found that there were positive effects of both mean egg volume and shape (Table 3). The interaction between egg volume and shape was non-significant ($F_{1, 73} = 0.181$, $p = 0.672$).

4. Discussion

Typically of birds, the eggs of Rollers were non-randomly similar to each other in egg-size traits within clutches, with most variation occurring among clutches (Ojanen *et al.* 1979, Bańbura & Zieliński 1990, 1998, Christians 2002). We found that the ratio of the volume of the largest individual egg to the smallest egg was 1.70, a value that is close to an average for different species of birds (Christians 2002). The scarce data on egg sizes collected for different European populations of Rollers, including Spanish and East European populations, show little variation with no apparent geographical pattern in mean values (Dementev & Gladkov 1951, Makatsch 1976, Hudec 1983,

Table 3. Relationship between hatching success (binomial response variable: the number of hatchlings in relation to clutch size) and per-clutch mean egg volume and shape of Rollers, tested using a generalized linear mixed model, with logit link function and year as a random factor. Random effects: SD = 6.502, residual SD = 1.0.

Covariate (X)	Estimate ± SE	$F_{1, 74}$	p
Mean egg volume	0.441 ± 0.135	10.71	0.002
Mean egg shape	0.191 ± 0.062	9.46	0.003

Nikisrorov *et al.* 1989, Hellmich 1995, Avilés *et al.* 1999). The mean egg length we found in Poland is well within this range, while mean breadth is slightly lower than the values reported in the literature. The mean volume is slightly larger than that reported by Avilés *et al.* (1999) for Spain.

We demonstrated that effects of clutch size on egg breadth and volume differed between years. In one year (1995) egg size increased with increasing clutch size, while in other years such relationships were non-significant. In view of the fact that in another year a tendency for a negative relation between clutch size and egg volume also occurred, the results generally fulfill our prediction that the reproductive allocation of resources in egg size and number may differ between years. Parejo *et al.* (2015) showed that in the Spanish population of Rollers, the weather during the one-month-long period prior to the onset of breeding generates varying fecundity selection on reproductive traits. The reason is that this period is critical for big insects that constitute the main food of Rollers. Because in our study population breeding starts in the second half of May, we checked what the weather was like between 16 April and 15 May in 1990–1996. It turned out that this period in 1994 (negative relation between clutch size and egg size) and 1995 (positive relation) were characterized by similar average temperatures, 10.6°C and 10.1°C, respectively. The values were in the middle of the range for all the study years, between 7.8°C and 14.7°C. In the pre-breeding period of 1995 also rainfall, 36.3 mm, was in the middle of the range for all years, 14.2–60.5 mm, while this period in 1994 was much drier, with the rainfall of 17.0 mm. This may suggest that the mild weather conditions in the pre-breeding period of 1995 were advantageous for insects and, therefore, Rollers, whereas

the drought in 1994 was disadvantageous. This seems to agree with the conclusion of Parejo *et al*. (2015) on a link occurring between fecundity selection on reproductive characteristics of Rollers, the weather conditions in the pre-breeding period and the availability of insects (Frampton *et al*. 2000). It seems probable that large beetles (Coleoptera) which are the most important component of the diet of Polish Rollers (Górski 2005) are most abundant in the mild, not extreme, weather conditions, especially with respect to rainfall (Frampton *et al*. 2000).

We think that the effects of year-clutch size interaction on egg traits we found corroborates the idea of Järvinen (1996) that between-year differences may mask the trade-off predicted by life-history theory (Smith & Fretwell 1974, Stearns 1992). The fact that at least in one year of our study the effect of clutch size on egg size was positive is in agreement with the female-quality (pair-quality) explanation for phenotypic correlations of life-history traits (Reznick 1985, Stearns 1992). Yet, we actually expected that the declining population of Rollers we studied was existing in non-optimal conditions where the trade-off should be often expressed, but only in one year a tendency for such a trade-off was found. A possible explanation of the disagreement between this expectation and our data is that because through 1980s and 1990s the process of the population declining was relatively slow and, assuming that good nesting territories were still available, the territories were probably occupied by high-quality, older pairs of Rollers, which would have led to obscuring the clutch size/egg size trade-off.

We found that the shape (sphericity) of Roller eggs was negatively associated with the timing of egg laying and positively with clutch size, without any effect of year or interactions with year. This may suggest that the sphericity of eggs is indicative for female quality, as earlier laying dates and producing larger clutches are typical of high-quality females (pairs) in birds (Perrins 1970, 1996). The fact that eggs are characterized by the shape corresponding to clutch size is also consistent with the optimal shape hypothesis proposed by Barta & Székely (1997), which does not exclude the female-quality (pair-quality) explanation. A possibility that egg breadth and length may undergo different pressures and show different patterns of variation was presented by Chylarecki (1993).

In general, the existence of a pattern of egg size and shape variation may have fitness-related consequences. The results of the study by Parejo *et al*. (2012) suggest that female Rollers may plastically invest resources in egg sizes under the influence of current trophic conditions. In a short-term perspective, the decreased hatching rate of small eggs generates a pressure on females to invest as much as possible into individual eggs (Krist 2011). The longer-term consequences of this initial selection are finally shaped during the nestling stage, when effects of hatching asynchrony, obligatory in Rollers, are revealed (Parejo *et al.* 2012).

In our study population of Rollers, hatching success proved also to be positively associated with egg sphericity in shape. It was previously shown by Parejo *et al*. (2012) that egg sizes positively influenced hatchability in a Spanish population of Rollers. Our finding of a positive effect of egg sphericity on hatching success is a novel result that supports the idea of Chylarecki (1993) that egg shape may influence the developing embryo. Although some positive influence of egg size traits on fitness was often postulated in avian research, the results were contradictory. The meta-analytic study by Krist (2011) proved that avian egg sizes indeed contribute to offspring fitness, with the influence being strongest at the earliest stages of offspring life.

Our study provides unique data on an important aspect of the breeding biology of a declining Roller population. It demonstrates that there are some consistent patterns in egg size and shape variation in relation to clutch size and that variation in egg traits may have consequences for fitness. Costs and benefits in terms of fitness are expected to mould the form of a relationship between egg sizes and clutch size and, therefore, variation in all egg traits. Our results are in general consistent with theoretical expectations, but we failed to find any specific links between egg size variation and the decline of the study population.

Munien kokovaihtelu
puolalaisilla sininärhillä

Teorian mukaan muodostuu kompromissisuhde pesyekoon ja poikasten koon välille kun rajallisia resursseja sijoitetaan jälkikasvuun. Kyseinen negatiivinen suhde ei välttämättä ole havaittavissa suotuisissa ympäristöoloissa, vaan saattaa ilmetä vain kun resurssit ovat vähissä. Tässä artikkelissa analysoimme munien kokomittojen vaihtelua suhteessa pesyekokoon puolalaisessa sininärhipopulaatiossa, joka taantuu maatalouden tehostumisen ja elinympäristöjen vähenemisen takia. Koska kevään sää vaikuttaa voimakkaasti suuriin hyönteisiin, oletimme että niiden runsaus – ja siten myös sininärhen ruuan saatavuus – vaihtelisi vuosien välillä säästä riippuen. Odotimme, että munien koon ja pesyekoon suhde, sekä munien mitat eroaisivat vuosien välillä, munimisajankohtaa edeltävän ajan ympäristön vaihtelua myötäillen. Oletimme myös, että munien koolla ja muodolla on jokin kelpoisuuteen liittyvä merkitys.

Tuloksemme osoittivat, että pesyekoon vaikutus munien kokoon vaihtelee vuosien välillä. Yhtenä vuonna suhde oli positiivinen ja toisena negatiivinen. Havaitsimme myös, että munien muoto oli pallomaisempi suuremmissa pesyeissä ja myöhäisemmissä pesinnöissä. Sekä munan koko että pallomaisuuden aste vaikuttivat positiivisesti kuoriutumisen onnistumiseen, vahvistaen ajatusta, että sininärhen munien piirteet vaikuttavat kelpoisuuteen. Tuloksemme ovat yleisesti ottaen teorian odotusten mukaisia, mutta emme löytäneet yhteyksiä munien koon vaihtelun ja tutkitun populaation vähenemisen välillä.

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