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Variation in egg and clutch size of the Black Redstart (*Phoenicurus ochruros*) at the northeastern edge of the Qinghai-Tibetan Plateau

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Abstract

Background: In birds, the trade-off between the quality and number of nestlings is one of the most important theories of the evolution of life history of birds, which is closely related with climate. We investigated variation in egg and clutch size of the Black Redstart (*Phoenicurus ochruros*) on the northeastern edge of the Qinghai-Tibetan Plateau in order to explore and test the relation between egg size and clutch size and the rules governing the variation in these two components with climate change.

Methods: We monitored each located nest daily to determine the exact laying order of the eggs and measured their sizes. The variations in egg volume and clutch size between 2008 and 2009 were studied by independent sample *t* tests. The difference in egg volume in the sequence of the laying order was tested by Kendall's *W* test and we employed Pearson correlations to investigate the relation between egg size and laying order. All statistical analyses were performed with IBM SPSS Statistics, version 19.0

Results: In 2008, the mean egg volume of the Black Redstart was 2.40 ± 0.20 cm^3 ($n = 50$), and the mean clutch size 4.90 ± 0.57 ($n = 11$). In 2009, the mean egg volume and clutch size were 2.26 ± 0.18 cm^3 ($n = 74$) and 5.20 ± 0.26 ($n = 15$) respectively. We found a significantly positive correlation between egg size and laying order ($r = 0.397$, $p = 0.030$), while egg size was strongly and negatively correlated with clutch size ($r = -0.274$, $p = 0.002$). Black Redstarts tend to lay smaller eggs but a larger clutch in a brood in a resource-rich year, whereas larger eggs but smaller clutches are produced in a harsh year.

Conclusions: The Black Redstart adopted a "brood survival strategy" to ensure that more offspring could survive. The Black Redstart' trade-off in egg volume and clutch size would guarantee that it will gain maximum benefit in any case.

Keywords: Egg size, Clutch size, Laying order, Trade-off, Black Redstart, *Phoenicurus ochruros*

Background

Right from the start of avian studies, investigators have focused on the ecology of eggs. Egg size varies greatly within many avian species, with the largest egg in a population generally 50% larger and sometimes even twice as large as the smallest (Christians 2002). In many bird species, egg size is often considered an important index of egg quality and is correlated with the survival of their offspring (Murton et al. 1974; Amat et al. 2001). Egg size can be adjusted in females with changes such as laying date (Hill 1984), female age (Desrochers and Magrath 1993), seasonal change (Coulson 1963; Du et al. 2012), laying order (Murphy 1994; Zhao et al. 2002a) or the condition of the female body (Hőrak et al. 1995), but no consistent conclusions about the effect of any of these factors have been drawn until now. Christians (2002) noted that although each of the above-referenced factors could explain part of the variation in egg size, these factors are not completely independent; therefore, it is possible

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that all these factors together could explain a great deal about the variation among females. Two strategies that most benefit parental gain in birds have been identified by Slagsvold et al. (1984). One strategy is the "brood-reduction strategy", i.e., a strategy that works mainly in species that hatch asynchronously, in which birds lay a relatively small final egg, where the final offspring will be sacrificed if food is insufficient. The other strategy is the "brood-survival strategy", in which birds produce a relatively large final egg, which could increase the probability that the offspring hatched from such an egg will be competitive with its elder siblings and fledge successfully. However, some birds, such as the Giant Babax (*Babax waddelli*), could mix brood reduction and brood survival strategies to maximize reproductive success depending on food availability (Du et al. 2012).

In birds, the variation in clutch size as an important strategy has gained the long-term attention of ornithologists (Lack 1947, 1948; Cody 1966; Simith and Fretwell 1974; Slagsvold 1982; Tinbergen and Daan 1990; Oppliger et al. 1997; Zhao et al. 2002b). The trade-off between quality and the number of nestlings is one of the most important theories of the evolution of life history, whereas clutch size represents the trade-off between the quality and the number of offspring of birds (Simith and Fretwell 1974; Winkler and Wallin 1987; Zhao et al. 2002b). Martin (1987) suggests that trade-offs also exist between clutch size and egg size, which means that females must lay a small clutch when she lays larger eggs or a large clutch when she lays smaller eggs. However, this trade-off has not been observed in a study of *Ficedula albicollis* by Hargitai et al. (2005). Christians (2002) reported that egg size appears not to be associated with clutch size within a species. Hence, there are different opinions concerning whether a trade-off exists between clutch size and egg size.

As well, the life history of birds has a close relation with climate. Over the past half century, studies of the impact of weather on the population biology of birds represent a major field of study for ornithologists (Crick 2004). Climate not only affects the metabolism of birds but also directly or indirectly affects the reproduction of birds (Zhao et al. 2002b; Crick 2004; Lu et al. 2007, 2008, 2010; Du et al. 2012, 2014). On the other hand, birds possess several mechanisms by which they can adjust the magnitude and pattern of their breeding effort in relation to environmental conditions and to their own breeding condition (Slagsvold et al. 1984). For example, weather can impact breeding success (Newton 1998). Extreme weather events, such as prolonged frozen spells and droughts, can have catastrophic effects on bird populations (Stenseth et al. 2002). White-bellied Redstarts (*Hodgsonius phaenicuroides*) inhabiting high-elevation environments have a shorter breeding period, smaller clutch size and larger egg size than their low-elevation counterparts (Lu et al. 2010). The relations among avian life-history traits is also affected by climate change (Both and Visser 2005). We have only begun to scratch the surface, although ornithology has provided some of the best examples of the impact of recent climate changes on wildlife from around the world (Lu et al. 2008). A range of intrinsic and extrinsic factors abound that could potentially inhibit adaptation to climate change. These factors are a high priority for research.

Hence, the purposes of our present study are: (1) to explore and test the relation between egg size and clutch size, two important components of the life history of birds and (2) to investigate the rules governing the variation in these two components with climate change. We expected to achieve these objectives by testing the variation between clutch size and egg size of Black Redstarts (*Phoenicurus ochruros*) during two successive breeding seasons (2008 and 2009) in a high elevation environment and by examining the relation of this variation with its ambient climate.

Methods

Study area

This study was carried out from 2008 to 2009 at the Gahai Protection Station (34°14′49″N, 102°20′44″E, elevation 3470 m), located at the northeastern edge of the Tibetan Plateau, in Gansu Province, China. The station is part of the Gansu Gahaizecha National Nature Reserve. The reserve has a typical Qinghai-Tibetan Plateau climate (low annual temperature but high annual precipitation, frequent sunshine and seasonally high winds), with an annual mean temperature of 1.2 °C (Liu and Ma 1997). Owing to plentiful precipitation (633–782 mm), the local landscape is an alpine meadow, with natural vegetation dominated by *Blysmus sinocompressus*, *Kobresia kansuensis*, *Cremanthodium stenoglossum*, *Pedicularis kansuensis*, *Potentilla anserine*, etc. (Liu and Ma 1997). Detailed characteristics are available in Du et al. (2014).

Data collection and statistical analyses

We systematically searched for nests during nest construction. We monitored each located nest daily to determine the exact laying order of the eggs; each egg was marked with a pen on the eggshell with its laying order for individual identification. This procedure did not appear to have any negative effect on the hatching. All eggs were measured with a Vernier caliper to the nearest 0.01 mm (maximum length and maximum width), with the egg volume (cm^3) calculated as $V = Kv \times L \times B^2/1000$, where Kv is a constant equal to 0.51, L is the maximum length (mm) and B the maximum width (mm) (Hoyt 1979).

The variations in egg volume and clutch size between 2008 and 2009 were tested by independent sample t tests. The difference in the egg volume according to the laying order was tested by Kendall's W test and the relation between the egg size and laying order by Pearson correlation (Dolenec 2006). The clutch size was classified as one of three types according to the clutch size: four, five and six eggs. Pearson correlation was used to examine the relation between egg volume and clutch size of these three clutch types. Temperatures and amounts of precipitation in March and April in 2008 and 2009 were obtained from the National Climatic Data Center.

All statistical analyses were performed with IBM SPSS Statistics version 19.0 (IBM Corporation, Armonk, New York, USA). Values are reported as mean ± SE, and $p < 0.05$ was considered statistically significant.

Results

Relation of egg size, clutch size and the variation of clutch size

In 2008, the mean length was 20.63 ± 0. 65 mm ($n = 50$) and the mean width 15.08 ± 0.57 mm ($n = 50$) for the eggs of the Black Redstart. Their mean egg volume was 2.40 ± 0.20 cm^3 ($n = 50$) and clutch size 4.90 ± 0.57 ($n = 11$). In 2009, the mean length was 20.32 ± 0. 99 mm ($n = 74$) and the mean width 14.74 ± 0.35 mm ($n = 74$). The mean egg volume was 2.26 ± 0.18 cm^3 ($n = 74$) and the clutch size 5.20 ± 0.26 ($n = 15$). Significant variations were found in the volumes between the 2 years ($t = 4.081$, df = 122, $p < 0.001$) (Table 1).

The mean clutch size in 2008 was 4.90 ± 0.57 ($n = 11$) (Table 1), in which, two nests contained four eggs, eight nests had five eggs and only one nest was found with six eggs. In 2009, 15 nests were investigated. Among these 15 nests, only one nest contained four eggs, 10 nests had five eggs and four nests contained six eggs; the mean clutch size was 5.20 ± 0.26 ($n = 15$) (Table 1). The mean clutch size was slightly larger in 2009 than that in 2008, but no significant difference in clutch size was found between the two years ($t = -1.304$, df = 23, $p = 0.205$) (Table 1).

Three classes of clutch size were identified in the Black Redstart in 2008 and 2009; these clutches were classified as four, five or six eggs, where clutches with five eggs accounted for the largest proportion (69.23%). The results indicate that the egg volumes in the three clutch sizes decreased in turn; that is, the volumes of the eggs from the nests with four eggs were largest, the volumes of the eggs from the nests with five eggs were intermediate and the volumes of the eggs from the nests with six eggs were smallest (Table 2). A negative correlation existed between the egg size and clutch size ($r = -0.274$, $p = 0.002$, $n = 26$).

Variation in egg size and laying order

Thirty eggs from six broods of the Black Redstart were measured with a Vernier caliper to the nearest 0.01 mm and egg volume was calculated using the following formula: V (cm^3) = $Kv \times L \times B^2/1000$. The results suggest that the egg volume increased with the laying order, with the mean egg volumes for the five eggs 2.24 ± 0.19, 2.23 ± 0.25, 2.31 ± 0.17, 2.34 ± 0.15 and 2.45 ± 0.17 cm^3, sequentially. Analysis of the 30 redstart eggs revealed a significantly positive relation among the volumes of the different eggs according to their laying order ($\chi^2 = 12.800$, $p = 0.012$, $n = 6$) and between the egg size and the laying order ($r = 0.397$, $p = 0.030$, $n = 30$).

Relation between eggs and weather conditions

Significant variations existed in the egg volume between the two years ($t = 4.081$, df = 122, $p < 0.001$) (Table 1). Although no significant difference was found in the clutch size between the two years ($t = -1.304$, df = 23, $p = 0.205$), the clutch size in 2009 was slightly larger than that in 2008 (Table 1). Nests with six eggs occurred more often in 2009 than in 2008, whereas the proportion of nests with four and five eggs decreased in 2009. Meterological data suggest that temperature and precipitation in March and April of 2008 and 2009 were different, with temperature lower and precipitation less in March and April of 2008 than in 2009 (Table 3). That is, the environment for early breeding in 2008 was harsher than that in 2009, as indicated by the smaller clutches with larger eggs in 2008 and larger clutches of smaller eggs in 2009 (Table 3).

Table 1 Egg volume and clutch size in different years

	2008		2009		t	p
	Mean	n	Mean	n		
Egg volume (cm^3)	2.40 (0.20)	50	2.26 (0.18)	74	4.081	0.001
Clutch size	4.90 (0.57)	11	5.20 (0.26)	15	−1.304	0.205

Values in brackets are standard deviations

Table 2 Egg volume in nests of different clutch sizes

Clutch size	Egg volume (cm^3)			Number of broods
	Mean	Standard deviation	*n*	
4	2.44	0.28	8	3
5	2.33	0.19	90	18
6	2.22	0.15	26	5

Table 3 Egg volumes and clutch sizes under different climate conditions

Year	Egg volume (cm^3)	Clutch size	March and April	
			Mean temperature (°C)	Mean precipitation (mm)
2008	2.40	4.90	0.85	15.05
2009	2.26	5.20	1.40	27.10

Discussion

Clutch size represents the trade-off between current breeding and future reproduction of parents and between the quality and number of offspring (Simith and Fretwell 1974; Winkler and Wallin 1987; Zhao et al. 2002b). Lack (1947) suggested that passerine birds should produce the largest number of offspring that can be successfully fed to breeding age by the parents. Therefore, he proposed that in most species, clutch size will ultimately be determined by the average maximum number of young the parents can raise, where the common clutch size or the average clutch size represents the maximum number produced (Lack 1947). This hypothesis is supported by several studies (Lack 1948; Högstedt 1980; Murphy 1994; Zhang et al. 2003; Crick 2004). In our study, the most common clutch size was five eggs (8/11 in 2008 and 10/15 in 2009). The average clutch size was 4.90 ± 0.57 and 5.20 ± 0.26 in 2008 and 2009, respectively (Table 1), with the average clutch size slightly larger in 2009 than in 2008; however, no significant difference was found between the 2 years ($t = -1.304$, df $= 23$, $p = 0.205$) (Table 1). The results indicate that five eggs represent the optimal productivity of the Black Redstart.

Females can vary their egg-size investment according to environmental circumstances, their own breeding condition and the quality of their mate (Hargitai et al. 2005). A few species begin to hatch eggs at the end of egg-laying and all the young then hatch together; while others have adopted a pattern termed "hatching asynchrony" (Clark and Wilson 1981), in which eggs begin to hatch before all the eggs are laid so that at least some of the young hatch before the others, often on successive days. The degree of asynchrony varies among species and sometimes within species (Viñuela 2000). Hatching asynchrony has generally been associated with the "Brood-reduction hypothesis" first advanced by Lack and Lack (1951) and Lack (1954). Several studies have suggested that size hierarchy would be more pronounced if the female investment in the final egg was decreased (Lack and Lack 1951; Lack 1954; Slagsvold et al. 1984). Therefore, when food availability is insufficient to raise all offspring, the smallest chick and the last-hatched, generally will starve quickly to increase the survival opportunity of its siblings (Lack 1954). In contrast, the "brood survival" strategy means females would reduce the disadvantages within a brood through more investment in the last-hatched offspring, by increasing the egg size with the laying order to ensure that more offspring can survive (Clark and Wilson 1981; Slagsvold et al. 1984). The Black Redstarts breeding in our study area seem to have adopted the "brood survival" strategy since a significantly positive correlation exists between egg size and laying order in that the volume of the eggs increased with the laying order and the final egg was generally larger than the others. The size hierarchy among nestlings within a brood was further decreased because the Black Redstarts begin to incubate at the end of egg laying and all young then hatch together.

Organisms may have a certain limited amount of time or energy available to expend and natural selection acts on the allocation of time or energy in a way that will maximize the contribution of a genotype to subsequent generations (Cody 1966). How to allocate this energy has led to the emergence of trade-offs between the benefits and risks under the guise of limited resources or capabilities. For example, is it the size of the clutch that determines the volume of the egg, or is the volume reduced because of the capacity of the female to reproduce limited? Our study on the Black Redstart indicates that egg size is negatively correlated with clutch size ($r = -0.274$, $p = 0.002$), which suggests a trade-off between these two life-history traits, i.e., the volume is smaller with a large clutch and vice versa. The investment of the female in these two interrelated characteristics is limited, which affects the emergence of this phenomenon. The females, therefore, have to make a trade-off between clutch size and egg size.

What leads to such a trade-off? One possibility is that females adjust their reproductive strategy according to their own situation; on the other hand, the trade-off may be triggered by environmental stress, with adjustments being made to accommodate offspring fitness. Williams (1994), after reviewing available research on the variation of egg size within species, noted the absence of unequivocal data to date in support of a positive relation between egg size and offspring fitness in birds. However, in his review, he did find a few studies that provided more consistent evidence of a positive relation between egg size and the fitness of offspring early in the chick-rearing period (Williams 1994). Therefore, he suggested that the most important effect of variation in egg size might be in determining the probability of offspring survival in the first few days after hatching (Williams 1994). Large eggs appear to have an advantage in harsh environments (Smith et al. 1995; Fox and Czesak 2000). On the Tibetan Plateau, elevation affects the breeding ecology of birds (Lu et al. 2007, 2008, 2010; Du et al. 2012, 2014) through the strong effects of temperature and rainfall, which also affect plant distribution and food availability. In our study area, temperature and rainfall were lower in 2008 than in 2009, suggesting that the climate in 2008 was harsher than in 2009 (Table 3). The disadvantages of low temperature and less precipitation would adversely affect the survival of the nestlings. The Black Redstarts adopted the strategy of laying larger eggs, which would improve the fitness of the nestlings under the harsh environment to recover the costs conferred by the environment (Smith et al. 1995; Fox and Czesak 2000). Therefore, because large eggs are produced in response to the harsher environment, a reduction in clutch size becomes a more favorable strategy, which can increase the input of each egg, whereas reducing the number of offspring can ensure that the offspring have a higher survival rate for future generations. Maybe under such harsh conditions, an increase in the number of eggs can lead to low quality in the entire clutch, with the final number of offsprings less than normal as more eggs might not be successfully hatched or offspring could not successfully fledge because of low quality. This circumstance remains to be further demonstrated. As for our study area, the environmental conditions were superior in 2009 and the advantage of laying large eggs could not be supported. Rather than wasting energy on fewer offspring, birds can increase the number of offspring, which will benefit from improved conditions so that a large clutch size and smaller eggs represent a good choice.

Conclusions

Given our results, the Black Redstart tends to produce smaller eggs but a larger clutch in a resource-rich year, whereas it produces larger eggs but a smaller clutch in a harsh year, which guarantees that the Black Redstart will gain maximum benefit in either case.

Authors' contributions

NL provided the research idea and designed the experiments. SS and JC conducted the experiments and collected the data. SS and JC finished the data analysis, compiled the results and wrote the first draft of the article. SS and BJ supervised the research and revised the draft. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Ethics statement

Our experimental procedures complied with the current laws on animal welfare and research in China and were specifically approved by the Animal Research Ethics Committee of Lanzhou University. The procedure used to mark the eggs with pens on the eggshell for individual identification and to measure the eggs with the Vernier caliper did not appear to cause any negative effect on the hatching.

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