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No evidence of weather effect found on the clutch size, eggs sizes and their hatchability in the red-backed shrike *Lanius collurio* in eastern Poland

Artur Goławski

Department of Zoology, University of Podlasie, Prusa 12, PL-08-110 Siedlce, Poland (e-mail: artgo1@ap.siedlce.pl)

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Weather conditions can influence birds' breeding performance through changes in metabolism of a female and can also directly affect eggs and chicks. I studied the influence of ambient temperature, variation in ambient temperature and rainfall on the breeding performance of the red-backed shrike *Lanius collurio* in 1999–2003 in the extensively agricultural landscape of eastern Poland. I did not find any influence of the analysed weather conditions on clutch size, mean egg volume in a clutch, variation of egg volume in a clutch and losses between the numbers of laid and hatched eggs. A probable explanation is that weather and food conditions are usually favourable for red-backed shrikes during egg laying and incubation, and males provide frequent supplemental feeding to the females at these stages of breeding. Probably, the extensively farmed agricultural area provides an abundant food base for the study population living there, which allows the red-backed shrike to quickly compensate its energy expenditures.

Introduction

Female birds are able to lay eggs because they store additional energy and nutrients needed for egg formation. This depends on food availability and suitable weather conditions (Martin 1987). Ambient temperature may change the energy status of laying in several ways: it may change the energetic cost of thermoregulation (Nager & van Noordwijk 1992, Tinbergen & Dietz 1994), or change food availability, especially of insectivorus species (Ojanen *et al*. 1981). As a consequence, the amount of energy that can be allocated to egg production may change (Järvinen 1991). Low temperatures during the egg-laying period may result in a smaller clutch size (Lack 1947, Cresswell & McCleery 2003). It is well known that egg size is positively correlated with ambient temperature (Järvinen 1991, Nager & van Noordwijk 1992, Perrins 1996, but *see* Tryjanowski *et al*. 2004). Egg parameters also result in certain consequences, as a greater number of eggs in a clutch is decisive in determining the number of nestlings, and larger eggs improve hatchability and fledgling survival (Williams 1994, Perrins 1996). Temperature also influences the timing of arrival and breeding phenology (Tryjanowski *et al*. 2002, Mitrus 2003, Ludwig *et al*. 2006). In addition to mean ambient temperature, metabolic rates are affected by the range of daily temperatures. This was demonstrated in laboratory studies on the Japanese quail *Coturnix japonica* (Pendlebury *et al*. 2004). Temperature variability can thus affect the energy budget in birds, which has consequences for reproduction parameters. This issue has been studied in the wild in only two species of passerines, and the results showed that temperature variability affected the size of eggs (Barkowska *et al*. 2003, Pendlebury & Bryant 2005).

The aim of this study was to determine how the breeding performance of the red-backed shrike *Lanius collurio* is affected by mean daily temperature, variation in mean daily temperature and rainfall. The first two factors affect birds' energy expenditures for thermoregulation, while rainfall strongly modifies the birds' food availability (Rodenhouse & Holmes 1992, Siikamäki 1996), and thus the chance to restore energy reserves. Weather is an especially important factor affecting the distribution of this species at the edges of its range. It is likely that the disappearance of the red-backed shrike in the UK was partly caused by changes in the weather, as even small changes in the frequency of sunny days may have catastrophic consequences for a population (Tryjanowski *et al*. 2006). Such small weather changes, when joined by deteriorating habitat conditions (agricultural development) and the resulting decrease in access to food (insects), can lead to very quick disappearance of a red-shrike population (Kuper *et al*. 2000). My study was conducted in an extensively agricultural landscape with great variability of insects (Goławski & Goławska 2008). The parametres of broods analysed were: clutch size, mean volume of eggs in a clutch, variation in egg volume in a clutch, and extent of losses between the number of laid eggs and hatched nestlings. The issue under study is important, as climate warming results not only in an increase in mean temperature, but also in greater variability of daily temperatures (Easterling *et al*. 1997). Until now, such studies have considered only sedentary species i.e. the great tit *Parus major* and the tree sparrow *Passer montanus* (Barkowska *et al*. 2003, Pendlebury & Bryant 2005). In contrast, the red-backed shrike is a long-distance migrant, which arrives at breeding grounds in Poland in the first half of May and starts breeding when ambient temperature is relatively high (Tryjanowski & Sparks 2001).

Material and methods

Study area

The study was carried out in eastern Poland, near Siedlce (52°12´N, 22°17´E) in 1999–2003. The study area consisted of 855 ha of extensively agricultural landscape. Arable fields predominated in this area (53.5%), mainly with crops of rye and potatoes. 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 and orchards. More details on the studied population, including aspects of breeding ecology and densities, have been published elsewhere (Goławski 2006a).

Bird data

I looked for red-backed shrike nests between mid-May and the end of July, checking all possible locations favourable for nesting. These places were monitored several times during the breeding season of the red-backed shrike. I measured eggs only in completed clutches ($N = 105$). The maximum length and breadth were measured with sliding callipers to the nearest 0.1 mm (all clutches measured by the author). I calculated the egg volume index (V) from the length (L) and breadth (B) using the formula re-scaled for red-backed shrike: $V = 0.5322LB^2$ (Surmacki *et al*. 2006). I also conducted the water test of egg fertility, which enables an estimate of hatching date to be made and excludes infertile eggs from further analyses (Mayer-Grosss 1972). I calculated the level of losses in clutches as the difference between the number of eggs in a clutch and the number of hatched nestlings. I determined the number of hatched nestlings on the date of hatching or the next day. I calculated the hatching date based on the time the first egg was laid and the number of eggs in the clutch. I assumed that red-backed shrikes lay one egg per day, begin incubating from the day of laying the penultimate egg, and continue incubation for 15 days (Cramp & Perrins 1993). I reduced the number of visits to the nests to the necessary minimum, as this species is especially vulnerable to disturbance and it often abandons clutches (Tryjanowski & Kuźniak 1999).

I analysed the influence of mean daily temperature, variation in mean daily temperature and the level of rainfall on the breeding performance of the red-backed shrike. The weather data were provided by the weather station of the University of Podlasie in the village of Zawady (ca. 20 km south of the study area). I calculated the mean and the variation in daily temperatures based on three measurements of the ambient temperature taken at 7:00, 13:00, 19:00 h with 0.1 °C accuracy (such measurements were available). I also used data on the 24-hour total amount of rainfall (with accuracy of 1 mm). I assumed that the clutch size and volume of eggs in the clutch should be affected by the weather of the week starting 4 days before the laying date of the first egg. Ambient temperature of the period distinguished in this way showed the strongest correlation with the red-backed shrike's clutch size during multi-year studies in central Poland (Diehl 1998). The variation in mean daily temperature and mean daily temperature in this period divided into five years differed significantly (ANOVA: $p < 0.001$, $N = 147$, in both cases), however differences in the level of rainfall were not significant (ANOVA: $p = 0.133$, $N = 147$). Weather conditions during incubation should be decisive for partial losses between the number of eggs in the clutch and the number of hatched nestlings. The weather conditions in the incubation period, analysed in this paper, divided into five years, differed significantly (ANOVA: $p < 0.001$, $N = 105$, in all cases).

I analysed the influence of weather conditions on breeding performance using the multiple regression method with the standard procedure (Sokal & Rohlf 2001). In this model, the dependent variables were, in turn: (1) clutch size, (2) mean volume of an egg in the clutch, (3) variation of eggs' volume in the clutch, (4) size of losses (clutch size *vs*. brood size). The independent variables were the mean daily temperature, variation in mean daily temperature and total amount of rainfall in a specific period (laying or incubation). I also added clutch size to the independent variables, as this could affect the other dependent variables listed (other than the first variable). During the analysis of weather influence on clutch size, I added a variable describing the starting date of breeding. I did so as I observed a decrease in clutch size as the season progressed in the studied population of the red-backed shrike (Goławski 2006a). Independent variables were square root transformed (after transformation $p > 0.05$). I used Statistica 6.0 (StatSoft 2003) software for statistical calculations.

Results

Mean ambient temperature in the period of egg laying varied between 12.1 °C and 24.2 °C, but SD was relatively small — only 16.3% of the mean value. The range of variance of ambient temperatures was from 0.4 °C to 29.5 °C (SD = 60.2% of the mean value). The sum of rainfall in this period showed the widest range for subsequent clutches (Table 1). The mean clutch size was 5.4 eggs. Despite large differences in the variance of ambient temperature and total rainfall between subsequent clutches, I did not find them to have an effect on clutch size (in all cases $p > 0.123$, Table 2). Among the analysed factors, the only one influencing clutch size was the date of clutch initiation (ANOVA: $F_{4,142} = 20.8$, $p < 0.001$, $R^2 = 35.2\%$), which explained 32% of the variation in clutch size.

The mean volume of an egg in a clutch was 3.0 cm^3 (Table 1). This parameter did not depend on weather conditions during the period of egg laying nor on the number of eggs laid (ANOVA: $F_{4,100} = 0.2$, $p = 0.909$). None of the analysed variables related to weather conditions showed a statistically significant effect on the mean volume of eggs (in all cases $p > 0.466$, Table 2).

The variance of egg volume in a clutch was very small — only 0.02 cm^3. This parameter was affected only by clutch size ($p = 0.001$) and explained 6.9% of differences in the volume of eggs (ANOVA: $F_{4,100} = 2.9$, $p = 0.024$). None of the analysed variables related to weather conditions showed a statistically significant effect on the variance in the mean volume of eggs (in all cases $p > 0.159$, Table 2).

The mean size of losses between the number of fertile eggs laid and the number of hatched nestlings was 0.4 eggs per clutch (Table 1). At least one egg did not hatch in only 29.1% of 55 analysed clutches. The ambient temperature calculated for the period of incubation varied between 13.6 °C and 22.1 °C, but SD was only 13.8% of the mean value. The range of the variance of ambient temperature was from 3.6 °C to 26.5 °C (SD = 59% of the mean value). The total rainfall in this period ranged widely for the compared clutches (Table 1). Despite this, weather condition did not influence the size of egg loss during the incubation period (ANOVA: $F_{4,50}$ =

Table 1. Reproduction parameters of the red-backed shrike and weather conditions in eastern Poland.

Variable	Mean	SD	Min	Max	*N*
Mean temperature in laying period (°C)	17.5	2.86	12.1	24.2	147
Mean temperature in the incubation period (°C)	18.6	2.56	13.6	22.1	55
Variation in temperature in laying period (°C)	9.8	5.9	0.4	29.5	147
Variation in temperature in the incubation period (°C)	11.7	6.9	3.6	26.5	55
Sum of rainfall in laying period (mm)	11.9	13.00	0.0	71.2	147
Sum of rainfall in the incubation period (mm)	22.5	18.38	4.8	78.6	55
Clutch size	5.4	0.83	3	7	147
Mean volume of eggs in a clutch (cm^3)	3.2	0.22	2.7	3.9	105
Variation in volume of eggs in a clutch (cm^3)	0.02	0.037	0.0008	0.32	105
Size of losses (clutch size *vs.* brood size)	0.4	0.74	0	3	55

Table 2. Results of multiple regression analysis of the breeding performance of the red-backed shrike against the weather conditions in eastern Poland.

Variable	*B*	SE	*p*
Clutch size			
Mean temperature in laying period (°C)	–0.126	0.172	0.465
Variation in temperature in laying period (°C)	–0.007	0.061	0.912
Sum of rainfall in laying period (mm)	0.044	0.029	0.123
Date of clutch initiation	–0.964	0.118	< 0.001
Constants	7.716	0.709	< 0.001
Mean volume of egg in the clutch			
Mean temperature in laying period (°C)	–0.017	0.066	0.797
Variation in temperature in laying period (°C)	–0.001	0.024	0.972
Sum of rainfall in laying period (mm)	–0.008	0.011	0.490
Clutch size	–0.021	0.028	0.466
Constants	3.377	0.364	< 0.001
Variation of eggs volume in the clutch			
Mean temperature in laying period (°C)	0.482	0.340	0.159
Variation in temperature in laying period (°C)	–0.057	0.125	0.646
Sum of rainfall in laying period (mm)	–0.030	0.057	0.599
Clutch size	0.497	0.147	0.001
Constants	–8.925	1.880	< 0.001
Size of losses (clutch size *vs.* brood size)			
Mean temperature in laying period (°C)	0.669	0.403	0.103
Variation in temperature in laying period (°C)	–0.075	0.125	0.554
Sum of rainfall in laying period (mm)	–0.024	0.069	0.731
Clutch size	0.211	0.159	0.191
Constants	–3.328	2.156	0.129

1.2, $p = 0.308$). None of the analysed variables related to weather conditions showed a statistically significant effect on the size of egg loss (in all cases $p > 0.103$, Table 2).

Discussion

I did not find any influence of weather conditions on clutch size, mean volume of eggs in a clutch, the variance of the volume of eggs in a clutch and losses of eggs during incubation. Clutch size depended only on the date of clutch initiation, which explained 32% of the variation in clutch size. The clutch initiation date has frequently been described as a factor that controls clutch size in the red-backed shrike (Kuźniak 1991, Goławski 2006a). It is probably connected with the earlier arrival of better quality or older and more experienced females, which can lay larger broods (Kuźniak & Tryjanowski 2003).

Weather conditions analysed in this study can affect birds' breeding performance through changes in females' metabolism. During a period of low temperatures, a female's metabolism increases and a lesser amount of accumulated energy reserves can be used for egg production (Tinbergen & Dietz 1994). This is demonstrated by the laying of smaller broods or smaller eggs (Järvinen 1991, Lessells *et al.* 2002, Cresswell & McCleery 2003), although not all studies confirmed such a relationship (e.g. Acquarone *et al.* 2003). Low temperatures can also affect the birds' ability to incubate laid eggs. Birds have to spend energy on their own survival and provide an appropriate temperature to the eggs. In the case of large clutches and low temperatures, extreme behaviour may occur, such as abandonment of broods or throwing some eggs out of the nest. Some cases of the death of the female on a nest during exceptionally adverse weather conditions have been recorded (Siikamäki 1995).

The variance of the temperature can also affect the energy expenditure of the female and influence brood parameters similarly to mean ambient temperature. This was demonstrated by studies on the tree sparrow and the great tit (Barkowska *et al.* 2003, Pendlebury & Bryant 2005). However, mean ambient temperature explained only up to 1.6% of the variation in the egg volume and the trend in temperature explained only up to 4% of the egg volume in the tree sparrow (Barkowska *et al.* 2003), while in the great tit these values were respectively 4.7% and 4.1% (Pendlebury & Bryant 2005). Thus, the values obtained were relatively low.

Weather conditions probably also influence the breeding performance of the red-backed shrike indirectly by reducing the availability of food for birds. The activity of the prey animals of the red-backed shrike strongly depends on the weather (Hornman *et al.* 1998, Kuper *et al.* 2000). During low temperatures and rainfall, birds' energy requirements increase (Nager & van Noordwijk 1992), and additionally they face difficulties in obtaining food. Thus, adverse weather conditions may have even greater influence on birds' broods. Abandonment of clutches in periods of unfavourable weather and nests being flooded by rain have been described (Jakober & Stauber 1980, Rudin 1990, Kuźniak 1991, Fornasari & Massa 2000). During my studies, some broods were also abandoned, but this resulted rather from the birds' timidity than from the influence of weather (Tryjanowski & Kuźniak 1999). I did not encounter any broods destroyed by rain.

The question arises then, why there was no relationship between weather conditions and the breeding performance of the red-backed shrike, despite a wide range of temperature variance and total rainfall. There are two possible explanations. Firstly, the analysed weather factors could be favourable for the birds anyway and thus did not largely affect females' energy expenditure. This could be confirmed by only a weak relationship (11% of explained variation) in the size of nestling losses from their hatching day to the 9th or 10th day of life, obtained during studies in this area (Goławski 2006b). Besides, energy expenditure could have been easily compensated by available food. The study area was an extensively used farmland, which provided a rich food base (Goławski & Goławska 2008). Invertebrates predominated in the food of red-backed shrikes in this area, and vertebrates, caught in greater numbers during periods of unfavourable weather (Hornman *et al.* 1998, Tryjanowski *et al.* 2003), comprised only 0.5% of the number of prey items (Goławski 2006c). This is also indirect evidence of favourable weather conditions for the red-backed shrikes during the five study seasons in eastern Poland. Greater food availability also decreased the egg-volume variation within the clutch of the bull-headed shrike *Lanius bucephalus* (Takagi 2003). Secondly, the males of the red-backed shrike intensively feed their mates during egg-laying and incubation periods. For example, during 48 hours of observations during incubation, the male fed the female on average 8.4 times per hour (Glutz von Blotzheim & Bauer 1993). In effect, energy expenses of the females for production or incubation of eggs can be compensated more quickly by food provided by the male, gained without any energy expenditure by the female. This can be particularly important during a period of limited prey availability. Mortality of embryos during incubation can be caused by temporarily ceasing egg incubation, i.e. when the female needs to feed. Warming up the eggs again costs the female a lot of energy, so that a strategy favourable for the higher hatchability of eggs should be the longest possible periods of uninterrupted incubation (Biebach 1979). Besides, evidence for a decrease of hatchability of eggs comes from studies in which the clutch size was experimentally increased (e.g. Moreno *et al*. 1991, Siikamäki 1995). Supplemental feeding of the female by the male in red-backed shrikes can minimise the effects of weather conditions on the number, volume and hatchability of eggs. It could be of importance that weather conditions were measured at the weather station located 20 km away from the study plot. However, in many other studies on the impact of weather conditions on breeding biology of birds weather data were collected from meteorological station located also 15–20 km away (Eeva *et al*. 2002, Lessells *et al*. 2002, Barkowska *et al*. 2003, Tryjanowski *et al*. 2004). Therefore, it could be assumed that the weather conditions registered at the station reflected well those at the breeding grounds. Hence, in could be concluded that favourable weather conditions best explain the results of my study. The eastern Poland is a center of the breeding area of this species of shrike and the size of the breeding population size is stable or even increasing (Dombrowski & Goławski 2002, Goławski 2006d).

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