

The influence of climate and population size on the distribution of breeding dates in the red-backed shrike (*Lanius collurio*)

Jan Hušek¹, Peter Adamík^{2,3}, Jaroslav Cepák⁴ & Piotr Tryjanowski⁵

¹ Department of Biology, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway (e-mail: jan.husek@bio.uio.no)

² Museum of Natural History, nám. Republiky 5, CZ-771 73 Olomouc, Czech Republic

³ Department of Zoology, Faculty of Science, Palacký University, tř. Svobody 26, CZ-771 46 Olomouc, Czech Republic

⁴ Bird Ringing Centre, National Museum, Hornoměřcholupská 34, CZ-102 00 Praha, Czech Republic

⁵ Department of Behavioural Ecology, Adam Mickiewicz University, Umultowska 89, PL-61-614 Poznań, Poland

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There are now a growing number of studies linking environmental conditions operating at different life stages of birds to their arrival on breeding grounds. Here we focus on one of the major fitness determinants; timing of breeding. We examined the influence of climate relevant to different parts of the birds' annual life cycle, and the impact of population size on distribution traits in a central European population of the red-backed shrike *Lanius collurio*. Timing of breeding was affected by breeding ground climate as well as by population size. In years with higher population densities shrikes started to breed earlier. In contrast to previous studies we did not find that our climatic variables adequately explained the variability of timing of breeding. We argue that density-dependent processes are also important for the reproduction of shrikes and that in phenological studies; attention should also be paid to other factors operating at breeding grounds.

Introduction

Climatic conditions have a wide range of impacts across the annual life cycle of birds. In the majority of studies, they were shown to influence arrival dates, timing of breeding, and population sizes in birds (Sæther *et al.* 2004, Gordo 2007, Newton 2007). The impact of climate on birds may be direct, e.g. ambient temperature or wind

speed and direction affecting body reserves of migrating birds (Newton 2007), or indirect, via changes to food resources (Jones *et al.* 2003, Gordo 2007, Pulido 2007). Events occurring at one life stage might have a prolonged effect on the individual's performance later in its life (Marra *et al.* 1998, Drent *et al.* 2006). It has been shown that conditions experienced in the wintering quarters (e.g. food availability) have

a direct effect on body condition and survival (Strong & Sherry 2000), causing birds in poorer condition to delay their departure (Marra *et al.* 1998, Norris *et al.* 2004). In addition, ecological conditions encountered en route may postpone migration, because leaner individuals would delay departure in order to obtain the fuel reserves necessary for self-maintenance during migration (Newton 2007). Condition-dependent arrival dates in migrants, i.e. when individuals in better condition arrive earlier than those in a poorer condition, have been documented in a range of avian taxa (e.g. Møller 1994a, Lozano *et al.* 1996, Marra *et al.* 1998, Kokko 1999, Drent 2006, Newton 2007). For example, Saino *et al.* (2004a) demonstrated that the arrival dates of barn swallows *Hirundo rustica* in Italy were earlier after winters with favourable ecological conditions in their African wintering quarters, and Møller (1994b) found in Danish barn swallows that the pattern of arrival to their breeding grounds was more variable in years with adverse ecological conditions in their wintering grounds, when many individuals in poor condition had presumably died.

These examples emphasize the potential links between conditions experienced by migratory birds in different phases and places of their annual activities. When considering changes in life-history traits that result from climate change, it is also essential to consider changes in environmental conditions affecting the whole annual life cycle, because there are interactions among different stages of the cycle (Coppack & Both 2003). However, studies linking all aspects are still quite rare (Gordo 2007, 2008, Newton 2007). Moreover, the majority of published papers have focused on early arrivals or on average arrival values (mean, median) which may not be representative of the whole population (Sparks *et al.* 2005, Knudsen *et al.* 2007). More detailed information is available from the shape of the frequency distribution of life-history traits, which implicates causes and consequences in the fitness of individuals. The shape reflects the distribution of condition-dependent arrival (Kokko 1999) and breeding dates, with resulting consequences in population demography. This is because, for example, female breeding strategies and the frequency of extra-pair paternities might be affected

by the form of the distribution of arrival dates. The frequency of extra-pair paternities depends also on breeding synchrony, which affects the intensity of sexual selection among individuals (Møller & Ninni 1998, Saino *et al.* 1999, Spottiswoode & Møller 2004), and the spread and symmetry of the distribution will affect the potential buffering of the reproductive output of the population. Overall, and most importantly, the shape of the distribution (skewness) and its changes could indicate selective pressures on life-history traits. Until recently, only a few studies have considered the possible role of climate change in influencing the shape of the frequency distribution of arrivals at breeding grounds (Ptaszyk *et al.* 2003, Sparks *et al.* 2005, Møller 2008a), breeding dates and clutch sizes (Winkler *et al.* 2002, Laaksonen *et al.* 2006). Laaksonen *et al.* (2006) found no clear trend in the skewness of laying dates during 1943–2003 in a Finnish population of the pied flycatcher *Ficedula hypoleuca*, a hole nesting species, but among-year variation in the skewness of laying dates increased and this appeared to be explained by variable temperature trends along the migration route. Skewness in clutch size appeared to change from more negative values to a more symmetrical distribution and variation in clutch size increased when wintering conditions were favourable. The distribution was then skewed with a tail of small clutches indicating that when ecological conditions during winter were good, low quality individuals were also able to breed (Laaksonen *et al.* 2006).

In this study, we analyzed the impact of climate from different parts of the annual life cycle and the impact of population size on breeding dates distribution in a Czech population of a long-distance migrant, the red-backed shrike *Lanius collurio*. Besides considering the effects of breeding ground climate on timing of breeding (Hušek & Adamík 2008), we also considered wintering ground climate and climate during migration. For migratory birds, climatic conditions encountered both on wintering grounds and during migration are important as they determine their physical condition (e.g. Marra *et al.* 1998, Bearhop *et al.* 2004, Saino *et al.* 2004b, Studds & Marra 2007), which results in variable arrival dates and condition on breeding grounds (Stolt & Fransson 1995, Sandberg & Moore 1996, Marra

et al. 1998). Arrival dates and physical condition of birds on breeding grounds then affect habitat occupancy as well as timing of breeding (e.g. Møller 2008b). We also considered the effects of intraspecific competition, as expressed by an index of population size, on timing of breeding. In summary, we assumed that the timing of breeding is influenced by condition and arrival dates mediated effects of wintering and migration ground climate, and by direct effects of breeding ground climate and effects of intraspecific competition.

Material and methods

Breeding data

For this study we used ringing data on red-backed shrike nestlings that were ringed during 1983–2006. In an earlier study we demonstrated that data obtained from ringing records are quite reliable and could be successfully used in phenological studies (Hušek & Adamík 2006). Hušek and Adamík (2006) showed that the mean number of ringed nestlings in nests at the time of ringing matched well with the mean number of nestlings from successful nests and that mean first laying dates strongly correlated with mean ringing dates. Annual ringing records of red-backed shrike nestlings for the Czech Republic were obtained from the Prague Bird Ringing Centre. We computerized information on the ringing of 36 076 nestlings from 8368 nests ringed during 1983–2006. We used the 10th percentile, median, skewness and variance of ringing dates as descriptors of timing of breeding for all clutches. The red-backed shrike is single-brooded, but when a first breeding attempt fails, replacement clutches are initiated. Thus, our dataset clearly contains unknown proportion of replacement clutches. Initiation of replacement clutches depends both on the rate and timing of first clutch failure (Antczak *et al.* 2009). Consequently, the proportion of replacement clutches mirrors various reasons of nest failure (predation, inclement weather) which are highly variable in both time and space. The values of nest failure of first clutches span from 11.3% (Horvath *et al.* 2000) through 23.6% (Pasinelli

et al. 2007) to 47.9% (Jakober & Stauber 2002) for shrikes during different time periods and at different study sites. In an attempt to avoid inclusion of replacement clutches we also performed the analyses with a truncated dataset. Considering roughly 25% of ringed nests at the end of the distribution to be replacement clutches each year, we defined first clutches as the 75th percentile of ringed nests annually for truncated dataset. We were cautious in inference from this dataset, as some varying proportion of replacement clutches might still have been included. Hence, the truncated dataset of first clutches consisted of 28 046 nestlings ringed in 6284 nests during the period 1983–2006. Similarly, the 10th percentile_{first}, median_{first}, skewness_{first} and variance_{first} of ringing dates were used as the “timing of breeding of first clutches” descriptors. Our ringing dataset dates back to 1964 but due to restriction in the availability of climatic variables (*see below*) we performed the analyses with 24 years only (*see Appendix*).

Climatic data

Wintering ground climate

As we were unable to precisely define particular wintering quarters of the Czech population (due to insufficient numbers of Czech ringing recoveries from Africa) and match them with finer-scaled climatic variables, we considered the shrikes' whole wintering range in eastern and southeastern Africa (Lefranc & Worfolk 1997).

Quite recently it was shown that the climate variability in East Africa is linked to the inter-annual sum of Indian Ocean sea surface temperature (SST) variations, termed the Indian Ocean Dipole (IOD; Marchant *et al.* 2007). The IOD represents the zonal dipole structure of the various coupled ocean–atmosphere parameters such as SST, surface pressure, outgoing long wave radiation and sea surface height anomalies (Yamagata *et al.* 2003). This unique independent ocean atmosphere coupled phenomenon in the Indian Ocean is characterized by anomalously warming of SST over the western Indian Ocean and anomalously cooling of SST in the eastern Indian Ocean which is associated with

rainfall and moisture supply into eastern and southern Africa (Saji *et al.* 1999). Intensity of the IOD is thus represented by anomalous SST gradient between the western equatorial Indian Ocean and the south eastern equatorial Indian Ocean. This gradient is named as Dipole Mode Index (DMI; Saji *et al.* 1999). When the DMI is positive, the phenomena referred as the positive IOD, an increased rainfall and moisture supply cause vegetation development over the tropical eastern Africa (Saji *et al.* 1999, Marchant *et al.* 2007). As insect abundance depends on plant productivity, positive values of DMI are in fact likely to influence physical condition and departure dates of shrikes via prey availability (*see* Studds & Marra 2007).

Shrikes arrive at wintering grounds in eastern and southeastern Africa in November and start to depart in the second half of March (Lefranc & Worfolk 1997). For the analysis of the influence of wintering ground climate on breeding parameters we thus used the mean of the Dipole Mode Index (DMI) for the months from November to March. The mean of the DMI from November to March covers the period of the shrikes' stay on the wintering grounds. The DMI data were obtained from Frontier Research Center for Global Change, Japan (available at <http://www.jamstec.go.jp/frsgc/research/d1/iod/>).

Migration route climate

Czech ringing recoveries provide some evidence that red-backed shrikes regularly pass through the Middle East during their northward migration (Cepák *et al.* 2008). We used mean temperature anomalies for April and May for Israel (hereafter T_{passage}), spanning the whole spring passage period. Northward spring migration of red-backed shrikes via Israel has two peaks, usually at the end of April and in the second half of May (Cramp & Perrins 1993). The area under consideration was defined by a grid 33°N, 30°N, 34°E and 36°E which covers most of Israel. The temperature data were obtained from National Climatic Data Center, Asheville, NC (available at: <http://www.ncdc.noaa.gov/gcag/gcag.html>). The correlation between T_{passage} and DMI ($r = 0.17$, $n = 24$, $p = 0.426$) was not significant.

Breeding ground climate

We used mean May temperature (T_{May} hereafter) and mean May precipitation (P_{May} hereafter) to study the effect of breeding grounds climatic factors. These consist of average values for the entire Czech Republic derived annually from more than 20 main meteorological stations. Data were provided by the Czech Hydrometeorological Institute in Prague. There was neither significant correlation between T_{May} and DMI ($r = 0.18$, $n = 24$, $p = 0.397$), between T_{May} and T_{passage} ($r = 0.29$, $n = 24$, $p = 0.169$), between T_{May} and P_{May} ($r = -0.26$, $n = 24$, $p = 0.221$), between P_{May} and DMI ($r = -0.26$, $n = 24$, $p = 0.214$) nor between P_{May} and T_{passage} ($r = -0.09$, $n = 24$, $p = 0.671$).

Population size data

Data on population numbers of the red-backed shrike in the Czech Republic were provided by the Czech Society for Ornithology. The population numbers are converted into an index of abundance (hereafter IA) and these data are based on a standardized national breeding bird monitoring program (Reif *et al.* 2006). There was no significant correlation between IA and number of ringed nests ($r = -0.13$, $n = 24$, $p = 0.546$).

Candidate models

Factors and the sets of candidate models were selected *a priori* based on their potential biological importance. Candidate models for measurement of central tendencies of timing of breeding (median, median_{first}, 10th percentile and 10th percentile_{first}) were built as follows: First, only breeding ground climatic conditions were supposed to influence the timing of breeding yielding model with factor T_{May} and model with T_{May} and year. Second, density-dependent processes were supposed to influence the timing of breeding alongside breeding-ground climate. We thus defined model with factors T_{May} and IA and model including T_{May} , IA and year. Third, we hypothesized the timing of breeding to be influenced by climatic conditions during the whole annual life cycle yielding model with

climatic factors from the breeding ground as well as from the wintering ground (T_{May} , DMI), model including also migration route climate (T_{May} , DMI and T_{passage}) and same models with the year effect were also included. Fourth, combination of the whole annual life cycle climate conditions and density-dependent processes on breeding grounds were considered in model with T_{May} , IA, DMI; model with T_{May} , IA, DMI, T_{passage} ; model with T_{May} , IA, DMI, year and global model with T_{May} , IA, DMI, T_{passage} , year. May temperature was included as covariate in all candidate models because of its known effect on the timing of breeding of first clutches (Hušek & Adamík 2008).

Variability of breeding dates of both all clutches (variance) and first clutches (variance_{first}) was supposed to be influenced by unfavorable breeding ground climate (model with P_{May} and model with P_{May} , year). P_{May} was chosen as a climatic descriptor here, because of known effect of rainy weather on nest failure in shrikes (e.g. Holáň 1994, Takagi 2001). Alternatively, density-dependent processes (model with IA; model with IA, year) were hypothesized to affect the distribution of the timing of breeding. Then, combination of breeding ground climate effects and density-dependent processes (model with P_{May} , IA; model with P_{May} , IA, year); whole annual life cycle climate (model with P_{May} , DMI; model with P_{May} , DMI, year; model with P_{May} , DMI, T_{passage} and model with P_{May} , DMI, T_{passage} , year) and combination of whole annual life cycle climate and density-dependent processes (model with P_{May} , IA, DMI; model with P_{May} , IA, DMI, T_{passage} ; model with P_{May} , IA, DMI, year and global model with P_{May} , IA, DMI, T_{passage} , year) were supposed. Finally we hypothesized the variance and variance_{first} to be affected by climatic conditions on wintering ground only (model with DMI; model with DMI, year), and by climatic conditions on wintering ground and density-dependent processes (model with DMI, IA and model with DMI, IA, year).

Candidate models for skewness and skewness_{first} were built, following the same hypothesis framework as for variance and variance_{first}, but T_{May} was used instead of P_{May} . The number of ringed nests was included as a covariate in candidate models because of its correlation

with variance_{first}, skewness, skewness_{first} and also variance (Table 1). Year was included as a continuous covariate in some candidate models to account for inter-annual variation and possible effects of temporal trends in the data.

Statistical analyses

Because breeding data are a time series, we examined the residuals (regressions on years) of all variables for the presence of autocorrelation. We used the Durbin-Watson test with the AUTOREG procedure of SAS 9.1 (SAS Institute 2004). None of the response variables were autocorrelated (all $D > 1.7$, $p > 0.18$). Therefore, we used each year's values as statistically independent observations.

We fitted general linear models with GENMOD procedure assuming identity link and normal distribution (SAS Institute 2004). An information-theoretic approach was used to examine which variables and models of an *a priori* defined set of candidate models best described the data (Burnham & Anderson 2002). Model selection was based on Akaike's information criterion corrected for small sample sizes (AIC_c ; Burnham & Anderson 2002). Akaike model weights, based on AIC_c were then calculated. Akaike weights are considered a measure of probability that a specific model best explains the data, given the set of all candidate models and they sum to one by definition. Model averaging was used for parameter estimation if no single model had Akaike weight > 0.9 . Akaike weights were calculated for individual variables as the sum of Akaike weights of all models in which the variable in question appeared. Model fit was checked with a residual analysis (McCullagh & Nelder 1989).

Results

General findings and correlations between distribution descriptors

During 1983–2006, the mean 10th percentile of timing of breeding of all clutches and first clutches was 165.73 ± 0.77 (\pm SE) and 164.70

Table 1. Pearson correlations between the distribution descriptors of the timing of breeding and ringing activity in the Czech population of red-backed shrike during the period 1983–2006 (r and p values in parentheses, $n = 24$ years). Variables denoted with subscript refer to a truncated dataset (for details see Material and methods). Significant correlations ($\alpha = 0.05$) are set in boldface.

	Median	Median _{first}	10th percentile	10th percentile _{first}	Variance	Variance _{first}	Skewness	Skewness _{first}
No. of ringed nests	-0.21 (0.323)	-0.08 (0.712)	0.04 (0.836)	0.04 (0.853)	-0.34 (0.107)	-0.40 (0.053)	0.39 (0.057)	-0.41 (0.047)
Median		0.94 (< 0.001)	0.76 (< 0.001)	0.74 (< 0.001)	-0.05 (0.817)	0.45 (0.029)	-0.57 (< 0.040)	-0.07 (0.753)
Median _{first}			0.88 (< 0.001)	0.85 (< 0.001)	-0.24 (0.259)	0.18 (0.415)	-0.36 (0.081)	-0.24 (0.263)
10th percentile				0.98 (< 0.001)	-0.39 (0.062)	-0.19 (0.364)	0.01 (0.957)	-0.14 (0.527)
10th percentile _{first}					-0.41 (0.048)	-0.19 (0.378)	0.02 (0.916)	-0.15 (0.487)
Variance						0.56 (0.002)	-0.44 (0.030)	0.42 (0.042)
Variance _{first}							-0.88 (< 0.001)	0.22 (0.293)
Skewness								-0.08 (0.710)

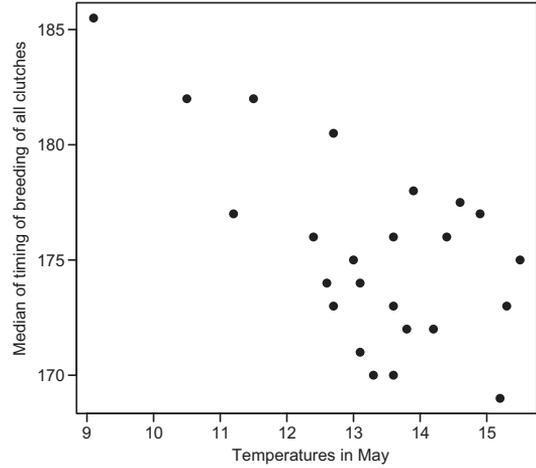


Fig. 1. Relationship between the median of timing of breeding of all ringed clutches (day 1 = 1 January) and mean May temperature in a Czech population of the red-backed shrike *Lanius collurio*.

± 0.73 , respectively (day 1 = 1 January). Mean median of all clutches and first clutches was 175.35 ± 0.87 and 171.98 ± 0.80 , respectively and mean variance of all clutches and first clutches was 135.31 ± 5.38 and 39.32 ± 3.16 , respectively. Distribution of the timing of breeding was usually positively skewed (i.e. having a concentrated range of values with a right hand tail) for all clutches (mean \pm SE = 0.95 ± 0.07), but was negatively skewed for only first clutches (-0.26 ± 0.10). Correlations between distribution descriptors from the whole and truncated dataset showed that all 10th percentile, 10th percentile_{first}, median and median_{first} were robust against truncating (Table 1). Obviously, these measures were not much hampered by including replacement clutches into the analyses. Skewness was significantly negatively correlated with the number of ringed nests, but correlation between variance and number of ringed nests was marginally not significant (Table 1).

Relationships of climatic factors and population size with timing of breeding

For the median, T_{May} , IA and year had Akaike weights > 0.85 (Tables 2 and 3). Median of all clutches was earlier with higher T_{May} ($b \pm$ SE = -2.05 ± 0.36 , Fig. 1) and with higher IA ($b =$

Table 2. Results of the model selection on factors influencing the timing of breeding in the red-backed shrike. All models contain an intercept term. Abbreviations: $\log L$ = maximum likelihood estimates, K = number of parameters, AIC_c = AIC value corrected for small sample size, ΔAIC_c = difference in AIC_c to the best model. Akaike weight (w_i) indicates measure of support of a model relative to all other models considered. Models are ranked according to Akaike weights and only models with $\Delta AIC_c \leq 3$ are presented.

Response variable	Model	$\log L$	K	AIC_c	ΔAIC_c	w_i
Median	T_{May}^y IA, year	-54.6	4	119.3	0.0	0.74
Median _{first}	T_{May}^y IA, year	-53.2	4	116.6	0.0	0.70
10th percentile	T_{May}^y IA	-57.1	3	121.4	0	0.30
	T_{May}^y IA, DMI	-56.0	4	122.0	0.7	0.22
	T_{May}^y IA, year	-56.2	4	122.6	1.2	0.17
	T_{May}^y IA, DMI, year	-55.2	5	123.8	2.4	0.09
	T_{May}^y IA, DMI, $T_{passage}$	-55.5	5	124.3	2.9	0.07
10th percentile _{first}	T_{May}^y IA	-55.6	3	116.3	0.0	0.57
	T_{May}^y IA, DMI	-54.2	4	118.6	2.3	0.18
	T_{May}^y IA, year	-54.6	4	119.2	2.9	0.13
Variance	No. of nests, P_{May}^y year	-106.0	4	222.1	0.0	0.24
	No. of nests, P_{May}^y DMI, year	-104.6	5	222.4	0.3	0.21
	No. of nests, DMI, year	-106.8	4	223.7	1.5	0.11
	No. of nests, IA, year	-107.5	4	225.1	3.0	0.05
Variance _{first}	No. of nests, DMI	-96.1	3	199.5	0.0	0.20
	No. of nests, P_{May}^y DMI	-94.8	4	199.8	0.3	0.17
	No. of nests, P_{May}	-96.5	3	200.3	0.8	0.13
	Intercept	-99.3	1	200.7	1.3	0.10
	No. of nests, IA	-97.2	3	201.6	2.1	0.07
	No. of nests, IA, DMI	-96.0	4	202.2	2.7	0.05
	No. of nests, DMI, year	-96.1	4	202.4	2.9	0.05
Skewness	No. of nests, T_{May}	-5.8	3	18.7	0.0	0.17
	Intercept	-8.4	1	18.9	0.2	0.15
	No. of nests, IA	-6.0	3	19.1	0.4	0.14
	No. of nests, DMI	-6.0	3	19.2	0.5	0.13
	No. of nests, T_{May}^y DMI	-5.2	4	20.6	1.8	0.07
	No. of nests, T_{May}^y IA	-5.3	4	20.8	2.0	0.06
	No. of nests, IA, DMI	-5.3	4	20.8	2.1	0.06
	No. of nests, T_{May}^y year	-5.8	4	21.6	2.9	0.04
Skewness _{first}	No. of nests, IA	-10.8	3	28.8	0.0	0.37
	No. of nests, IA, year	-10.3	4	30.7	2.0	0.14
	No. of nests, T_{May}^y IA	-10.5	4	31.2	2.4	0.11
	No. of nests, IA, DMI	-10.8	4	31.7	2.9	0.09

Table 3. The Akaike weights of individual explanatory variables over all models in which the variable in question was included. Covariate values are in parentheses.

Response variable	Explanatory variables						
	T_{May}	P_{May}	DMI	IA	$T_{passage}$	Year	No. of ringed nests
Median	(1.00)	–	0.20	0.98	0.05	0.93	–
Median _{first}	(1.00)	–	0.21	0.99	0.05	0.88	–
10th percentile	(0.99)	–	0.49	0.88	0.13	0.32	–
10th percentile _{first}	(0.99)	–	0.29	0.95	0.07	0.17	–
Variance	–	0.69	0.56	0.22	0.08	0.80	(0.97)
Variance _{first}	–	0.50	0.60	0.24	0.05	0.17	(0.90)
Skewness	0.44	–	0.39	0.32	0.03	0.14	(0.84)
Skewness _{first}	0.27	–	0.23	0.83	0.01	0.27	(0.95)

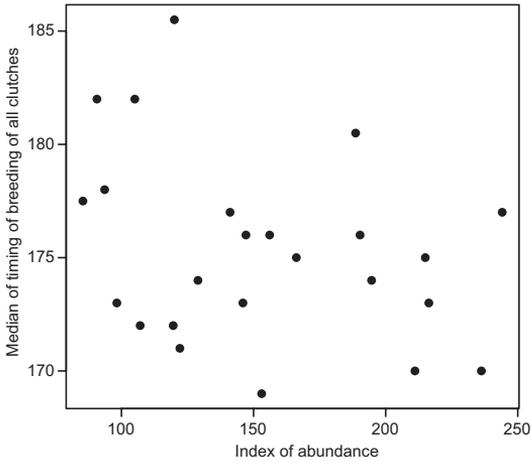


Fig. 2. Relationship between the median of timing of breeding of all ringed clutches (day 1 = 1 January) and index of abundance in a Czech population of the red-backed shrike *Lanius collurio*.

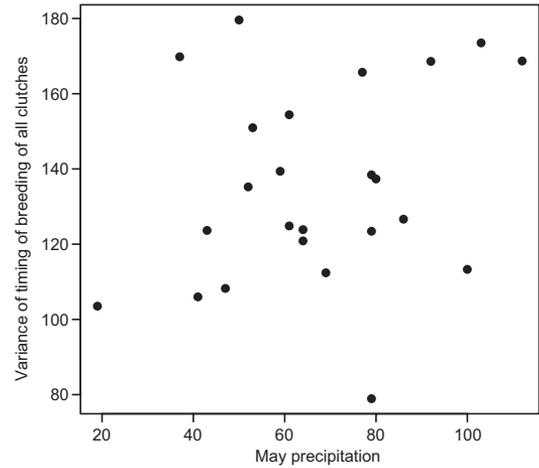


Fig. 3. Relationship between the variance of timing of breeding of all ringed clutches and May precipitation in a Czech population of the red-backed shrike *Lanius collurio*.

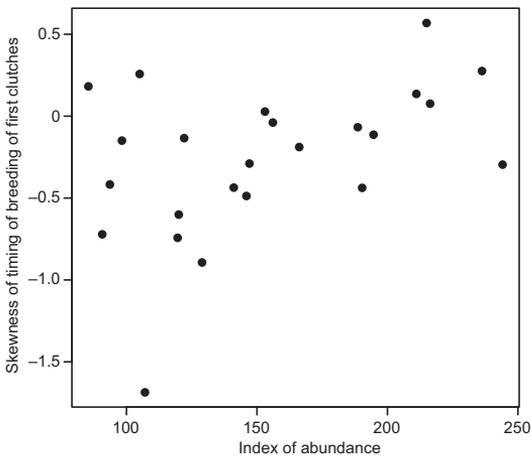


Fig. 4. Relationship between the skewness of timing of breeding of first clutches and index of abundance in a Czech population of the red-backed shrike *Lanius collurio*.

-0.06 ± 0.02 , Fig. 2) but slightly delayed over the study period ($b = 0.29 \pm 0.13$). Principally the same results were found for the median_{first} (T_{May} : $b \pm \text{SE} = -1.87 \pm 0.34$; IA: $b = -0.06 \pm 0.02$; year: $b = 0.24 \pm 0.12$). Similarly, the 10th percentiles for the whole and truncated dataset yielded similar parameter estimates (10th percentile; T_{May} : $b \pm \text{SE} = -1.33 \pm 0.38$; IA: $b = -0.03 \pm 0.02$ and 10th percentile_{first}; T_{May} : $b \pm \text{SE} = -1.28 \pm 0.34$; IA: $b = -0.03 \pm 0.01$; Table 2). However, there was no evidence for

effect of year on either 10th percentile or 10th percentile_{first} over the study period (Tables 2 and 3).

A weak effect of climatic variables and population size was found for variance, where only P_{May} ($w_i = 0.69$) and year ($w_i = 0.80$) had some weights in explaining it (Tables 2 and 3). Variance tended to increase over the study period ($b = 1.60 \pm 1.06$) and tended to be higher with higher P_{May} ($b = 0.26 \pm 0.32$, Fig. 3). Only DMI had some weight ($w_i = 0.60$) in explaining variance_{first} (Table 3).

No variable affected the skewness of all clutches (Tables 2 and 3). For skewness_{first} only the IA had Akaike weight > 0.80 besides the number of ringed nestlings (Table 3). The negatively skewed timing of breeding of first clutches tended to become positively skewed with an increase of IA ($b = 0.003 \pm 0.002$, Fig. 4).

Discussion

In this study, we found that the timing of breeding of a central European population of the red-backed shrike was influenced both by spring temperatures and population size. We highlight the effects of population size on timing of breeding and suggest considering also other relevant factors in studies of climatic effects on avian phenology.

During 1983–2006 the distributions of the timing of breeding of the red-backed shrike were mostly positively skewed for all ringed nests. This is because right-hand tail (positive skewness) of all clutches contains also replacement clutches. On the other hand, when only first clutches (i.e. truncated dataset) were considered, the distributions of the timing of breeding were mostly negatively skewed. Left hand tail of distribution of first clutches mirrors the onset of breeding, when a few exceptionally early breeders start to breed early. These could represent birds in better condition which are able to start breeding soon after their arrival (Newton 2004) and earlier than the bulk of the population. Earlier nesting individuals then have better reproductive performance (e.g. van Noordwijk & de Jong 1986, Sheldon *et al.* 2003), which was also shown for early nesting red-backed shrike pairs (Kuźniak 1991, Müller *et al.* 2005, Hušek & Adamík 2008). However, it must be noted that pronounced negative skewness in breeding dates with left hand tail of breeders tends to be overestimated in our study, because most probably among the first breeders there is also a tail of individuals in inferior condition, which were cut away among the 25% when analysing the truncated dataset.

The timing of breeding was affected by both breeding ground climatic conditions and by intensity of intraspecific competition processes as approximated by population size. The timing of breeding measured as medians and 10th percentiles was earlier when May temperature was higher for both all clutches and first clutches. Additionally, medians of timing of breeding in both datasets slightly delayed over the study period. No such effect was found for the 10th percentiles. Variance of timing of breeding of all clutches also slightly increased during 1983–2006. Spring temperature during the onset of breeding plays an essential role in shrike's breeding phenology. Shrike has advanced both its timing of arrival, as well as the timing of breeding in central Europe since the 1960s/1970s (Tryjanowski & Sparks 2001, Hušek & Adamík 2008, Z. Hubálek unpubl. data), latter due to an increase in the mean May temperature. Here the pattern of slightly delaying medians and growing variance in timing of breeding might be caused

by increasing proportion of replacement clutches in recent years, but this hypothesis should be tested in future studies.

We found that beside the breeding ground climate, population densities also affected the timing of breeding. With a higher population size, medians and 10th percentiles were earlier for all clutches as well as first clutches. This finding is also supported by the influence of population size on skewness of timing of breeding of first clutches, which makes it even more robust. Skewness of timing of breeding of first clutches turned from being negatively skewed to being positively skewed with higher population size. This means that larger proportion of individuals starts to breed earlier when population size is higher. Higher population densities are likely to lead to more intense intraspecific competition; as a consequence, birds may be forced to start breeding earlier (for general discussion of the subject *see also*: Møller 2008a).

Both (2000) hypothesized that the pattern of density-dependent breeding dates is more common in resident than in migratory species, and he found no density dependence in either breeding date or clutch size in a long-distance migrant, the pied flycatcher. However, we argue that density-dependent processes also affect the timing of breeding and that they are important for reproduction in the open nesting red-backed shrike (*see also* Müller *et al.* 2005). Overall, we found that the timing of breeding is not only influenced by climatic conditions encountered within the birds annual life cycle (Laaksonen *et al.* 2006), but also by density-dependent processes.

In contrast to previous studies (Winkler *et al.* 2002, Laaksonen *et al.* 2006), we did not find evidence that our climatic variables adequately explained the variance of timing of breeding of first clutches. Only the precipitation in May and year had some power in explaining variance of timing of breeding of all clutches. Variance of all clutches increased with more precipitation in May indicating that inclement weather causes some first nesting attempts to fail. This is in agreement with previous findings on sensitivity of nesting shrikes to inclement weather (Holáň 1994, Takagi 2001, Goławski 2006, Hušek & Adamík 2008, but *see* Goławski 2008). The

effect of individual bird condition (e.g. Sæther *et al.* 2004, Stokke *et al.* 2005, Robinson *et al.* 2007) on variability of timing of breeding of first clutches, as indicated by some weight of DMI in explaining it, should be further tested in shrikes.

In conclusion we demonstrated that ringing data could successfully be used in bird phenological studies on a large scale (*see also* Hušek & Adamík 2008). However, using ringing data for more detailed studies in bird populations is likely to be problematic and is possible only for local populations of abundant species if these are ringed in sufficient numbers and when sufficient information is recorded about ringed nestlings.

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Appendix. Distribution descriptors of timing of breeding in red-backed shrike used in the analyses (day 1 = 1 January).

Year	Median	Median _{first}	10th percentile	10th percentile _{first}	Variance	Variance _{first}	Skewness	Skewness _{first}	No. of nests
1983	171	169	165	164	78.94330	15.67765	1.513403	-0.134182995	266
1984	182	178	172	171	123.44595	48.13900	0.66678	0.25768871	329
1985	172	169	163	162	138.42143	36.82396	0.803776	-0.743165111	322
1986	177.5	171	163	163	168.67865	78.40801	0.435844	0.181330793	352
1987	182	178	171	169.2	113.32208	43.35672	0.50621	-0.721672931	410
1988	172	170	164	164	105.99063	30.15133	1.207336	-1.685905088	606
1989	174	171	165	164	108.24919	28.42940	0.989095	-0.112759247	672
1990	173	170	165	164	123.63688	30.67766	1.028991	-0.148980681	502
1991	185.5	183	174	172	123.86160	40.85216	0.717597	-0.600978414	251
1992	178	175	170	169	103.52768	27.39473	1.227695	-0.417035044	454
1993	173	172	166	163	135.22858	25.25677	1.250338	-0.487773524	576
1994	174	173	167	167	112.40147	23.63873	1.107453	-0.893401769	517
1995	176	173	168	167	126.65863	27.41329	1.495698	-0.437444572	542
1996	173	169	165	164	173.51784	35.57413	1.221015	0.075751459	562
1997	170	166	162	161	120.87322	29.00237	1.465975	0.275430613	402
1998	170	166	159	158	169.82196	47.72002	0.771947	0.135964422	334
1999	176	173	167	165	179.61133	43.52002	0.83594	-0.038583618	281
2000	177	175	169	168	124.84227	34.15261	1.187967	-0.436465884	303
2001	176	171	163	161.7	154.39451	57.53593	0.581077	-0.289997217	250
2002	175	172	162.6	161.5	150.95610	55.28023	0.580776	-0.188660415	358
2003	169	166	161	161	165.70125	25.78246	1.252214	0.027828556	180
2004	177	172	161	160	139.37148	62.90132	0.490196	-0.295633822	184
2005	175	171.5	168.9	168	137.34058	30.71725	1.062065	0.568908536	156
2006	180.5	174	166	165.3	168.57940	65.32202	0.406176	-0.067483165	221