

Local weather differently affects collared flycatcher reproduction at different altitudes

Research Article

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Abstract: Temperature and precipitation are amongst the most important characteristics of local climatic conditions affecting the breeding biology of birds. Many bird species experiencing higher temperatures lay their eggs earlier and/or have bigger clutches. Higher precipitation can lead to a decrease in food availability and/or an increase of the costs of thermoregulation, which consequently may result in lower breeding success. In this paper we present differences in the breeding biology of two collared flycatcher (*Ficedula albicollis*) populations experiencing different temperatures and precipitation conditions associated with the different altitudes of their localities. We found differences in clutch size and nest success, as well as small differences in dates of egg laying. The population breeding at a higher altitude, and thus harsher conditions, was characterized by smaller clutches and lower nest success. In addition, this population was significantly affected by local weather, and showed correlation between both the beginning of egg laying and the local temperature, as well as between nest success and precipitation. Conversely, the population inhabiting the lower elevation locality with milder conditions showed no relationships with temperature or precipitation. These results suggest that severe conditions, such as high altitude, enhance the effect of local climatic conditions on collared flycatcher breeding ecology.

Keywords: Breeding success • Breeding season • Egg laying • Clutch size • Temperature • Precipitation

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1. Introduction

Climatic factors such as temperature and precipitation are amongst the most important factors affecting breeding ecology of birds. Variation in temperature and precipitation has impact mainly on breeding phenology [1-3] and breeding success [4,5], but evidence also shows the effect of weather conditions on variation in bird body size [6,7], clutch size, egg mass and quality [8], and nest construction [9].

However, not all variation in phenology and breeding biology can be explained simply by climatic fluctuation;

some differences could be linked to species-specific ecology and/or life history [10-12]. Also, populations in optimal conditions are usually less sensitive to annual changes in temperature or precipitation, whereas populations breeding in suboptimal habitats usually show higher variation in their ecology [13,14].

Here we address the differential effects of local climatic conditions on two collared flycatcher [*Ficedula albicollis* (Temminck, 1815)] populations breeding at different altitudes over multiple years. The collared flycatcher is a hole nesting insectivorous passerine species which commonly breeds in woodland habitats of

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Central and Eastern Europe [15]. It is a migratory species which nests willingly in nest boxes at high densities, and is known to reflect environmental differences associated with altitudinal variation [16,17], which makes the species an ideal model for a comprehensive long term study. Although the collared flycatcher can breed at altitudes of up to 1.100 m a.s.l. in the region of Central and Eastern Europe, conditions characterizing such altitudes are considered sub-optimal, whereas deciduous forests at lower elevation (up to 500 m a.s.l.) are considered optimal [18].

Our aim in this study is to test the influence of temperature and precipitation on reproductive characteristics of the collared flycatcher such as egg laying dates, clutch size, and nest success. We hypothesize that the population experiencing more severe conditions at a higher altitude would be more affected by weather than population breeding under optimal conditions.

2. Experimental Procedures

Breeding biology of the collared flycatchers was studied in two nest box populations inhabiting localities at different altitudes in central Slovakia. Altogether we analyzed 394 broods. The lower elevation population (LA=lower altitude; 280-400 m a.s.l.) was studied in Horná Nitra (N 48°39', E 18°35') during the years 2001-2011, and the locality of the higher elevation population (HA=higher altitude; 630-670 m a.s.l.) was situated about 60 km more easterly in the region of Kremnické Vrchy Mts. (N 48°40', E 18°55'), and was studied during the years 2007-2011. The habitat of both localities was formed by managed deciduous forests of a similar tree composition dominated by oaks (*Quercus petraea*), beeches (*Fagus sylvatica*) and hornbeams (*Carpinus betulus*) with rare firs (*Abies alba*) and pines (*Pinus silvestris*).

To eliminate potential effect of variable hole/nest size on breeding biology [19,20], we used wooden nest boxes with similar internal dimensions (12×12×25–30 cm), and single entrance holes 3.2 cm in diameter. These were spaced at similar heights of 2.5–3.5 m. The number of boxes varied between the study sites and also increased during the study period. All nest boxes were regularly monitored every 7–10 days during the breeding season to record the beginning of egg laying, clutch size and nest success. Nest observations were as short as possible with the perturbation of eggs/nestlings/parents kept to a minimum to avoid stressing the parents, which could potentially lead to nest abandonment and decreasing nest success.

We characterized the beginning of the egg laying by two variables: 1) first egg date (FED = date when the first clutch in a particular year was initiated), and 2) the median laying date (MLD = median initiation date of all the first clutches at the locality in a particular year). Nest success was estimated by Mayfield method [21]. Exposure of successful nests was terminated on the day when nestlings reached the age of 16 days, whereas the exposure of nests with uncertain fate was terminated on the last check when the nest was still active. The midpoint between the last active day of a nest and the first check after the nest failure was used as a date defining termination of the exposure in unsuccessful nests [22].

Nests which were obviously destroyed by predators (most often dormice *Glis glis* and *Muscardinus avellanarius* and Great Spotted Woodpecker *Dendrocopos major*) or occupied by other species (Wryneck *Jynx torquilla*) before fledging were excluded from the nest success estimates.

Local weather characteristics, temperature and precipitation, were obtained from the nearest weather stations in Prievidza (LA) and Kremnické Bane (HA) situated ca 15 and 7 km, respectively, from the study sites. Altitudes of weather stations were similar to study plots (280 m a.s.l. in LA and 780 in HA). We used average April temperature to test its influence on the beginning of egg laying and average May and June temperatures and precipitation values to test their possible effects on the nest success.

We performed correlation analysis and general linear model regressions (GLM) to test for the relationships between breeding parameters and climatic factors (temperature, precipitation) [1,2]. Since the population at the LA locality was monitored for longer period than the population at HA locality, we built two datasets – one comprising data for all years in both localities, and another limited to the data from years 2007-2011. The analyses were run separately for both datasets. The results were generally the same (see Table 1), therefore we only refer to the results obtained from the full dataset. The comparison of temperature and precipitation between localities and years, as well as the comparison of breeding parameters between LA and HA populations and research years was carried out using parametric one way ANOVA with Bonferroni correction. Overall year nest success between localities was compared using Mann - Whitney U test. All analyses were carried out with Statistica 8 (Statsoft; Tulsa, OK) software.

3. Results

The LA locality is characterized by higher temperature and lower precipitation than HA locality (Table 2).

	Lower-elevation population (LA) (Horná Nitra) 2001-2011						Lower-elevation population (LA) (Horná Nitra) 2007-2011						Higher-elevation population (HA) (Kremnické vrchy Mts.) 2007-2011					
Variable	predictor	df	r	R ²	β	P	df	r	R ²	β	P	df	r	R ²	β	P		
First egg date	temperature	10	-0.5129	0.2630	-1.50	0.130	4	-0.4827	0.2330	-1.29	0.410	4	-0.9899	0.9798	-0.54	0.001		
	precipitation	10	-0.1698	0.0288	-0.01	0.639	4	-0.0321	0.0010	0.00	0.959	4	0.5068	0.2569	0.00	0.383		
Median-laying date	temperature	10	-0.2756	0.0759	-0.42	0.441	4	-0.4430	0.1962	-0.58	0.455	4	-0.9315	0.8677	-1.16	0.021		
	precipitation	10	-0.0245	0.0006	0.00	0.946	4	0.1584	0.025	0.01	0.799	4	0.6651	0.4424	0.01	0.221		
Clutch size	temperature	10	-0.4437	0.1969	-0.11	0.199	4	-0.5394	0.2909	-0.13	0.348	4	0.7912	0.6260	0.20	0.111		
	precipitation	10	-0.3845	0.1478	0.00	0.273	4	-0.5720	0.3272	0.00	0.314	4	-0.8623	0.7435	0.00	0.060		
Nest success	temperature	10	0.3883	0.1508	3.91	0.268	4	0.5505	0.3031	5.38	0.336	4	0.4126	0.1703	1.13	0.490		
	precipitation	10	0.4218	0.2722	-0.13	0.122	4	-0.4232	0.1791	-0.13	0.478	4	-0.9115	0.8308	0.04	0.031		

Table 1. Results of the linear regressions of egg laying dates, clutch size, and nest success, and their climatic predictors during the study period.

		Temperature (°C)					Precipitation (mm)				
		average	sd	min	max	median	average	sd	min	max	median
Lower-elevation population (LA) (Horná Nitra)	2001	9.8	2.35	1.5	15.3	9.8	5.20	6.33	0	17.60	2.9
	2002	9.6	3.69	-0.3	14.4	10.2	5.9	5.87	0	22.7	3.7
	2003	9.1	5.72	-1.7	21.6	10.5	4.5	5.44	0	19.8	1.7
	2004	11.4	3.2	4.4	18.8	11.1	8.1	10.56	0	39.4	4.3
	2005	10.9	3.1	3.8	16.1	11.1	2.9	2.59	0	9.2	2.6
	2006	10.8	3.32	4.4	16.4	10.5	4.3	4.8	0	14.7	2.1
	2007	11.8	3.26	6.8	17.8	11.7	5.3	6.76	0	26.1	2.1
	2008	10.9	3.14	4.7	17.5	10.9	5.3	8.15	0	33.3	2.3
	2009	14.5	1.66	10.2	16.8	15.1	5.8	6.42	0	22.2	4.1
	2010	10.1	3.29	4.3	17.5	9.7	7.8	8.61	0	41.1	4.9
	2011	12.2	2.96	5.9	18.2	12.2	4.4	5.15	0	17.9	2.4
Higher-elevation population (HA) (Kremnické vrchy Mts.)	2007	8.5	3.33	2.3	14.2	8.2	7.3	7.88	0	33.7	4.3
	2008	7.2	3.02	2.4	13.5	7.4	5	5.71	0	23.7	2.6
	2009	10.7	1.72	6.4	14.4	10.9	4.6	4.95	0	18.6	2.8
	2010	6.7	3.47	1.5	14.1	6.3	10.5	11.78	0	46	5.3
	2011	8.7	3.45	1.6	14.6	8.8	8.2	7.93	0	24.1	5.8

Table 2. Average April temperature and average precipitation during May and June in two studied localities of collared flycatcher (*Ficedula albicollis*) during the study period.

The average April temperature in LA was higher by 3°C [$F(1,448)=60.284$, $P<0.001$] and the average precipitation during May and June was lower by more than 2 mm [$F(1,438)=5.059$, $P=0.025$] during the years of study. The average April temperatures differed between the years in both regions [$F(9, 290)=5.78$; $P<0.001$ and $F(4, 165)=7.61$; $P<0.001$ in LA and HA, respectively]. However, we found no between-year variation in precipitation in LA [$F(9, 272)=1.51$; $P=0.142$] and only weak variation in HA [$F(4, 153)=2.36$; $P=0.056$]. The between year significant difference in temperature is primarily caused by higher temperatures in the year 2009 on both localities (with a significant difference in comparison to the years 2002–2010 in LA and to the years 2008 and 2010 in HA).

We found no significant temperature increase during the study period at either locality ($r^2=0.332$; $P=0.08$ and $r^2=0.0004$; $P=0.97$ in LA and HA, respectively) and no positive or negative trends in rainfall amounts ($r^2=0.062$; $P=0.48$ and $r^2=0.411$; $P=0.24$ in LA and HA, respectively). The correlation between April temperature and precipitation was -0.19 in HA ($r^2=0.0372$) and -0.18 in LA ($r^2=0.0312$).

Collared flycatcher is the dominant breeding species at both studied localities and the total breeding pair density across the years ranged from ca 4 to 8 breeding pairs (BP) per one ha. The populations at lower altitude

(LA) and at higher altitude (HA) do not significantly differ in their first egg dates [$F(1, 14)=0.83$; $P=0.3745$] or median egg laying dates [$F(1, 323)=0.54$; $P=0.4631$], however the first egg laying in LA occurred ten days earlier (17th April) than in HA (27th April) and the mean first egg day in LA was one day earlier (27th April) than in HA (28th April; Table 3). However, both populations were characterized by between-year variation in median laying date [$F(10, 250)=7.22$; $P<0.0001$ and $F(4, 59)=5.22$; $P=0.001$ in LA and HA, respectively]. Thus we limited our comparison to the same period for both localities; i.e. the years 2007 to 2011, and a significant difference [$F(1, 8)=6.13$; $P=0.0384$] was found between localities (26th April and 28th April for LA and HA, respectively). The between-year variation in clutch size showed significance in LA [$F(10, 288)=3.18$; $P<0.0001$ with significantly higher clutch size in 2008 compared to 2009 and 2010], while not in HA [$F(4, 58)=2.27$; $P=0.07$]. The mean clutch size was higher in LA than in HA (Table 3), but the comparison showed no significance [$F(1, 360)=0.97$; $P=0.3258$]. We recorded no differences in overall nest success between the two populations ($z=0.23$; $P=0.81$), whereas the reproductive output of flycatchers breeding in LA was higher than in HA after we excluded the depredated broods ($z=2.29$; $P=0.02$).

None of the predictors explained the existing variation in first egg date, median laying date, clutch size, or nest

Locality	Year	Laying dates			Clutch size			Nest success		
		FED	MLD	n	average	min.	max.	n	NS	n
Lower-elevation population (LA) (Horná Nitra)	2001	120	122	9	6.2	5	7	10	63.09	11
	2002	115	121	11	6.6	5	8	12	62.36	13
	2003	119	122	17	6.3	4	7	19	64.76	21
	2004	120	125	12	5.6	3	7	19	49.36	21
	2005	119	125	24	5.8	3	7	21	89.89	24
	2006	121	125	18	5.9	3	8	19	56.54	25
	2007	107	119	22	6.1	3	8	23	88.79	24
	2008	116	121	27	6.8	4	10	29	58.09	31
	2009	110	119.5	32	5.7	3	7	42	75.08	45
	2010	116	123	38	6.0	3	7	50	51.39	53
	2011	117	124	51	6.2	4	7	55	83.89	57
Higher-elevation population (HA) (Kremnické vrchy Mts.)	2007	118	122	9	6	5	7	8	68.06	9
	2008	119	123	8	5.9	5	7	7	70.12	8
	2009	117	119	15	6.2	5	7	14	67.85	16
	2010	119	124	19	5.2	3	7	21	59.24	21
	2011	118	123	13	6.1	2	8	15	64.96	15

Table 3. Laying dates (in Julian dates), clutch size, and nest success in two studied populations of collared flycatcher (*Ficedula albicollis*). FED – First egg date, MLD – Median laying date, NS – Nest success (Mayfield estimation) during the study period.

success in LA (Table 1). However, we found significant negative effects of temperature on first egg date and median egg date in HA and significant negative effects of precipitation on nest success at the same locality (Figure 1; Table 1). The model testing for the effect of precipitation on clutch size resulted in a statistical output just outside of the significance threshold ($P=0.06$; Table 3) indicating potential importance of this predictor.

4. Discussion

Our results revealed that the breeding characteristics of the collared flycatcher are generally concordant with populations from other parts of Central Europe. This is true for the first egg date and median laying date [1,16,17,23], and also for clutch size and nest success [24,25]. However, in comparison to more northerly regions, such as Poland or Scandinavia, the laying was advanced [2,26–28].

Differences in egg laying in collared flycatcher populations during recent decades with regards to changing temperature conditions are known from other parts of Europe, and are usually explained by increased temperature associated with climate change [1,3,6,29]. This is supported by the overall correlation between the change of local spring temperature and egg laying

dates [30,31]. However, it seems that this relationship is not generally applicable for all species and has several exceptions [32]. In addition, this relationship can differ among different populations of the same species inhabiting various parts of the range [10,33]. We found no advancement in egg laying phenology of collared flycatcher at either of the studied localities. Although limited sampling could play some role in explaining the lack of this relationship [34], it is known that in some species the initiation of egg laying could be more affected by local conditions than by overall climate changes [33]. Also, species with broader distribution ranges can attain higher intraspecific variation at different localities than two species breeding in the same region [10]. Our results show that the collared flycatcher displayed differences in eggs laying, and was affected by local temperature at higher altitude (but not in the lower altitude); these results are in overall concordance with these previous findings. They also suggest that the population breeding in less optimal conditions is not only characterized by differences in breeding phenology, but is also more sensitive to variation in annual temperatures. This hypothesis is supported by data from breeding biology of collared flycatcher and its close relative pied flycatcher (*Ficedula hypoleuca*) from more than 20 European regions, where the impact of different temperature to phenology and clutch size was more prominent in the

populations breeding at sites with higher temperature fluctuations than in a stable environment. In addition, the egg laying date of collared flycatcher populations was more affected by temperature in northern part of the range (Sweden) than in more southerly located populations (Hungary) [29].

As expected, the breeding success of collared flycatcher population in HA was lower than in LA, most probably due to colder and moister weather during the breeding period. Changing weather can strongly affect food availability and the cost of thermoregulation [35] and rainfalls in breeding season could directly lead to the nest failure [36]. There are numerous studies revealing strong negative impact of precipitation during the breeding season on nest success of several bird species [4,5]. The impact of inclement weather can be especially severe in those species that feed their nestlings on insects whose availability is strongly dependent on weather conditions [37].

Similar to egg laying, we not only found differences in nest success between the two populations from different altitudes compared here, but we also revealed differences in the impact of weather on nest success. Breeding at higher altitude was negatively influenced by precipitation, but in contrast, the population at lower altitude was characterized by higher breeding success which was not influenced by precipitation. Therefore we hypothesize that the climate impact on the nest success could vary among optimal and suboptimal habitats. This is supported by the fact that collared flycatcher is a species that experiences relatively high mortality of nestlings in the years when it starts to lay eggs later [38]. Timing of breeding is usually well synchronized with phenophases of insects which form the major food source of the species [38,39], and delays in egg laying caused by spring temperature fluctuations can lead to decreased food amounts and lower breeding output [39,40]. At the HA locality, a similarly important factor negatively influencing the food availability in some seasons was colder and moister weather which most probably decreased the activity and thus availability of the insects.

Stronger effect of temperature fluctuations on breeding success in less optimal conditions compared to optimal habitats has already been reported for several bird species. For example, from two breeding populations of the white stork (*Ciconia ciconia*) in Slovenia, the weather characteristics explained a significant part of the variation in numbers of fledged chicks per pair only in the population with poorer food resources [13].

This offers a potential explanation for the variation observed in studied collared flycatcher populations.

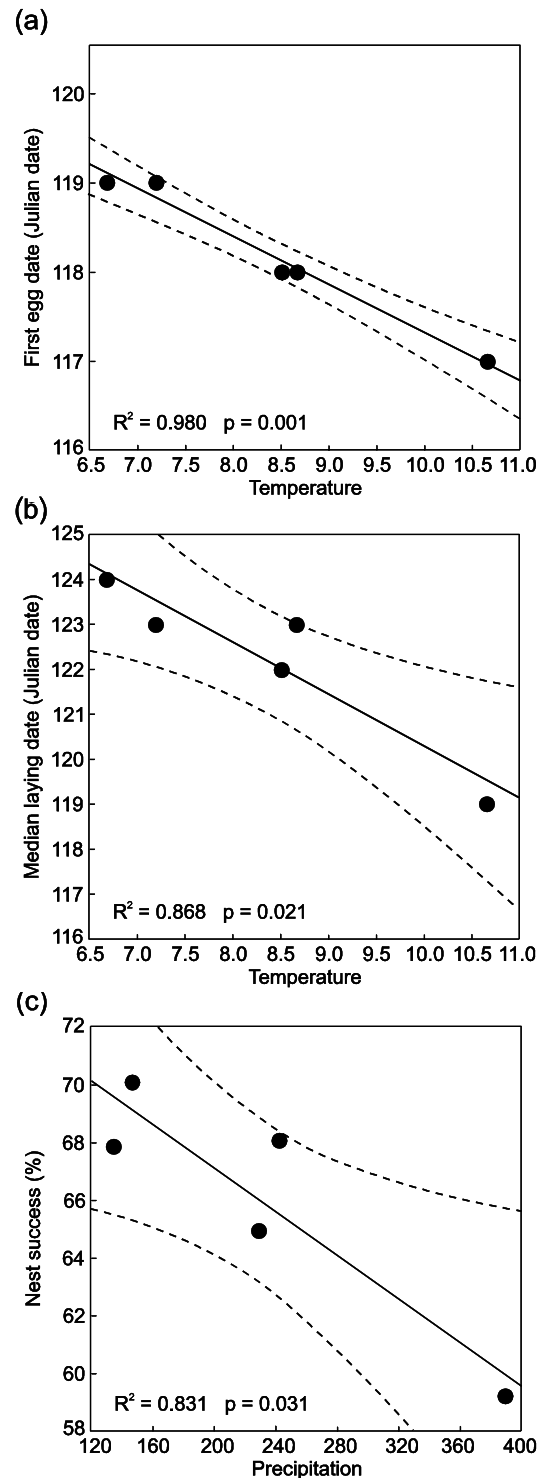


Figure 1. Relationships between temperature (°C) and first egg day (a), temperature and median laying day (b), and precipitation (mm) and nest success of the collared flycatcher (*Ficedula albicollis*) population breeding at higher elevation (HA) region Kremnické vrchy Mts. Dashed lines demarcate the 95% confidence interval.

Costs of adaptation to more severe conditions at higher altitude, such as lower temperature, higher precipitation during the breeding season, and higher between-year variation in precipitation may explain not only lower reproductive output, but also why this population is more sensitive to the varying climatic conditions than the population inhabiting the less harsh environment.

Taking all this together, we found that the collared flycatcher population breeding at lower altitude commences egg laying earlier, has bigger clutches and nest success, and is more resistant to weather fluctuation than the population breeding at higher

altitude. Although comparing only two populations with limited dataset may result in false conclusions [see 34], we hypothesize that our finding can be used in broader scale of species ecology.

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