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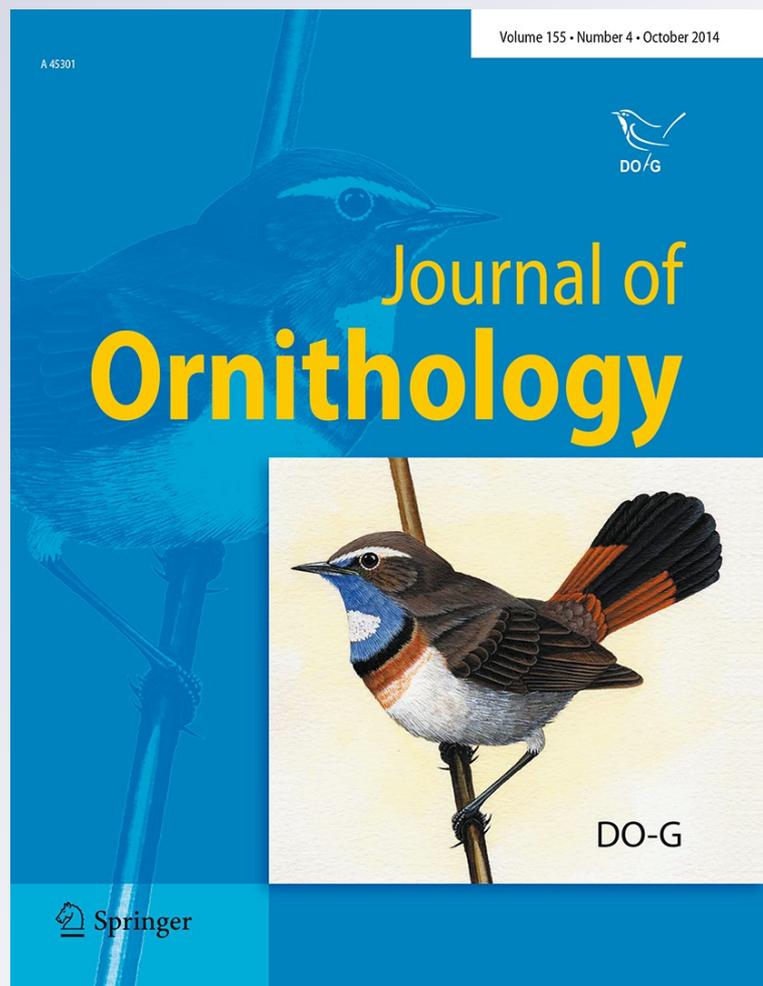
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Variation and long-term trends in the timing of breeding of different Eurasian populations of Common Redstart *Phoenicurus phoenicurus*

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Abstract Changes in the timing of reproduction of birds should provide good evidence of large-scale climate fluctuations. However, geographically separate populations of one species may respond variably. We analyzed egg laying dates of nine Eurasian populations of the Common Redstart *Phoenicurus phoenicurus* collected between 1969 and 2010. The timing of breeding differed greatly with latitude: the populations in the north started later, a breeding pair produced only one brood per season and the breeding season was shorter. Both yearly minimum and median first-

egg laying dates advanced with increases in local air temperature, but the more northern populations had started at much lower temperatures, which was probably caused by the stimulation of photoperiod. The effects of large-scale climatic patterns (North Atlantic Oscillation, East Atlantic, Scandinavia/Eurasia-1) on the first-egg laying date were low. The egg laying dates advanced over the observed decades in all populations, although at a variable rate. Seven selected populations with the most complete data for the period 1986–2010 revealed an advancement of median first-egg laying dates of 0.11 days/year and 1.31 days/°C. The effect on minimum first-egg laying dates was smaller. The changes observed in two populations in Ural and western Siberia were smaller than those found in more westerly populations (Finland, central Europe). The timing

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of the start of breeding is probably less affected by climate change than the timing of spring migration, documented by European ornithological stations.

Keywords *Phoenicurus phoenicurus* · Common Redstart · Climate change · Laying date · Timing of breeding

Zusammenfassung

Variation und langfristige Trends im zeitlichen Ablauf der Brut von verschiedenen eurasischen Populationen des Gartenrotschwanzes *Phoenicurus phoenicurus*

Änderungen der Fortpflanzungszeiträume von Vögeln sollten gute Hinweise auf großräumige Klimaschwankungen geben. Allerdings können geographisch getrennte Populationen einer Art unterschiedlich reagieren. Wir werteten die Eiablagedaten von neun eurasischen Populationen des Gartenrotschwanzes aus dem Zeitraum 1969–2010 aus. Der Brutzeitraum unterschied sich mit dem Breitengrad erheblich: Populationen im Norden beginnen später, ein Brutpaar hat nur eine Brut pro Saison und die Brutsaison ist kürzer. Sowohl die jährlich Frühsten wie auch die mittleren Ersteiablagedaten verfrühten sich mit Erhöhung der lokalen Lufttemperatur, wobei die nördlicheren Populationen schon bei deutlich niedrigeren Temperaturen anfangen, was vermutlich mit einer Stimulation durch die Tageslänge zu erklären ist. Die Auswirkungen von großräumigen Klimamustern (North Atlantic Oscillation, East Atlantic, Scandinavia/Eurasia-1) auf die Ersteiablagetermine waren gering. Der Zeitpunkt der Eiablage verfrühte sich bei allen beobachteten Populationen im Verlauf des Beobachtungszeitraums, allerdings mit unterschiedlicher Geschwindigkeit. Bei sieben ausgewählten Populationen mit den umfangreichsten Datensätzen für den Zeitraum von 1986 bis 2010 lässt sich eine Verfrüfung des mittleren Zeitpunkts der ersten Eiablage um 0.11 Tage/Jahr und 1.31 Tage/°C erkennen. Die Auswirkung auf den frühesten Zeitpunkt der ersten Eiablage war geringer. Die Veränderungen, die in zwei Populationen im Ural und in Westsibirien beobachtet werden konnten, waren geringer als bei weiter westlich gelegenen Populationen (Finnland, Mitteleuropa). Der Brutbeginn ist möglicherweise weniger vom Klimawandel als vom Zeitpunkt des Frühjahrszugs abhängig, wie er von europäischen Beobachtungs- und Beringungsstationen dokumentiert wird.

Introduction

Warm springs over the past few decades have been affecting the yearly biological rhythm of many bird species (e.g. Gordo 2007). A shift in the timing of one event may cause a chain of further consequences that can result in changes in the dynamic

of whole populations (Jiguet et al. 2010). In migratory species, the variables affecting the timing of migration and arrival to the breeding ground may be different from those affecting the start of breeding. The ecological answer of a species varies from one population to another, probably in connection with different migration routes (Hüppop and Winkel 2006), temperature, and conditions in the breeding area (Visser et al. 2003) or local photoperiod (Lambrechts et al. 1997).

There are not many studies that have analyzed long-term variation of the breeding dates in different geographically separate populations of the same species. Strong negative effects of local temperature and other weather variables on the mean date of egg laying have been discovered (flycatchers *Ficedula*, Sanz 2003; Both et al. 2004). However, the studies also revealed that these effects are sensitive to a geographic locality, and even that there were marked differences in the start of the breeding season among populations occurring close together (tits *Paridae*, Visser et al. 2003).

In our study, we have analyzed long-term breeding data of nine populations of Common Redstart (*Phoenicurus phoenicurus* ssp. *phoenicurus*) located in central Europe, Finland, and Russia up to western Siberia. The Common Redstart is a long-distance migrant and belongs to the most often encountered species in the monitoring of bird migrations in Europe. Several studies have discovered a strong effect of varying weather conditions (e.g. air temperature, precipitation, North Atlantic Oscillation index—NAO) on the timing of its spring migration or its arrival in Europe (Hüppop and Hüppop 2003; Stervander et al. 2005; Zalakevicius et al. 2006). Consequently, along with increasing temperatures in the past few decades there was a shift to earlier dates of mean spring passage time (e.g. Hüppop and Hüppop 2003). The start of the breeding of the Common Redstart is related to local air temperature and environmental conditions (e.g. Ruiter 1941; Järvinen 1983; Porkert and Zajíc 2005; Kuranov 2007), but the species seems to be quite tolerant to temperature fluctuations as the eggs were laid and incubated even under low extremes in northern populations (Järvinen 1990; Pulliainen et al. 1994; Veistola et al. 1996).

The aims of our study are (1) to determine the differences of the start and distribution of broods during a season in different geographical populations of the species, and (2) to discover the long-term trends in the start of breeding of these populations. We hypothesize that the onsets of breeding seasons are parallel to the change of the timing of migration that was observed over the past decades.

Materials and methods

Study species

The Common Redstart is a small insectivorous passerine. The nominate subspecies, which is the subject of our study,

is spread almost continually throughout all of Europe, in the Atlas Mountains in northern Africa, and to the east up to the Lake Baikal in Asia (Hagemeijer and Blair 1997; del Hoyo et al. 2006). It mainly lives in the temperate forest zone and its further distribution to northern or arid biotopes is limited by the presence of trees. The main breeding biotope is open forest land, as well as town parks and orchards. Its wintering areas are south of the Sahara and in the Arabian Peninsula (Cramp 1988; Kristensen et al. 2013). Despite the lack of a definitive study, it seems that the breeding population splits into two main migration routes. The redstarts from Scandinavia and western and central Europe migrate to the west crossing the Mediterranean Sea across Spain, while populations from eastern Europe, Siberia, and some populations from Finland fly over Italy, the Balkan Peninsula, or the Middle East (Hope Jones 1975; Zink 1981; Glutz et al. 1988; Wernham et al. 2002; Cepák et al. 2008). There are two autumn migration records of redstarts ringed as juveniles in the Tomsk region in western Siberia (population included in our analysis, Table 1: ID 5). Both birds were heading west, one checked in western Russia north of the Black Sea and the second in Syria (S.G., unpublished data). The spring migration to the breeding grounds is generally more direct than the autumn migration (Hope Jones 1975; Kristensen et al. 2013). Redstart males arrive to breeding grounds several days earlier than females (e.g. Menzel 1984). Nests are placed in cavities on the ground, rocks, buildings, or in trees, and often in artificial nest-boxes. The birds in the southern and central parts of the distribution range may breed twice per season.

Data on breeding

The data included in our study were collected from nine populations chosen from different parts of the species distribution range (Table 1; Fig. 1). The co-authors were contacted by the first author directly after previous publications or through bird ringing stations. We used existing data sets. The conditions for inclusion were the existence of data on the laying of first eggs of broods covering at least 10 years over the period 1990–2010 and a minimum number of six records of first/regular broods per season. Data for all populations originate from study sites with artificial nest-boxes. The information of nest-box design, total nest-box occupancy and the proportion of the most abundant breeding species (>3 %) were summarized (Online resource Table A1). The surplus of empty nest-boxes in all studied populations probably eliminates the competition for nest place, which could have been affecting the start of breeding. Nests were checked usually every five days or more frequently. The laying date of the first egg in a nest was determined based on the observation of egg laying sequence. In the cases of

later nest discovery (either during the incubation or chick-feeding), the first-egg laying date was calculated according to the assumptions based on the breeding biology of the species (Menzel 1984; Cramp 1988; Glutz von Blotzheim et al. 1988). These were: one egg is laid each day until the clutch completion; egg incubation starts on the day when the last egg is laid; incubation lasts for 14 days; age of nestlings up to 10 days can be estimated according to their body development.

We first plotted the data of all years of observation together to illustrate the timing and distribution of broods in individual populations (Fig. 2a–i). Second broods (i.e. the broods following the successful first broods) and/or replacement broods (i.e. the broods following the unsuccessful first broods) were determined in some populations (Fig. 2a–e, g), however, the method of data collection was not designed to estimate the second brood proportions. In further analysis, all broods known as second or replacement broods, or broods that started later than 30 days after the minimum start date of a season were excluded as not the true first breeding attempts (Visser et al. 2003; Both et al. 2004). Only the years with six or more records left after the above procedure were included in further calculations. In order to get a more comprehensive information on the species distribution area, one population was included, although not fulfilling the condition of a time period (population ID 3). An observation period of another population (ID 9) was split into two parts (9a for the year period 1969–1984 and 9b for 1986–2008) to match the start of the second part with the other time series.

Weather data

Local air temperature was used for testing the small-scale effect on the redstart breeding. Mean daily temperatures were obtained from meteorological stations nearby the study sites. We computed mean air temperatures at the mean minimum first-egg laying dates of each population (T_{\min}) in the analyses where the means of whole observation period of a population were used as replication variables (Table 1; Fig. 3, Online resource Table A2).

Where the replication was each year in each population (Tables 2, 3; Fig. 4a, b, Online resource Tables A3, A4), we used temperatures from the time interval related to the start of breeding in the first five years of each data set. We used the 30-day period before the mean of the median laying dates of the five years (Both et al. 2004; Weidinger and Král 2007). The mean value of the 30-day period was used as the year temperature variable. Means of temperature of three, five, and 10 days before the day with started broods were used for testing the short-term temperature effect (Online resource Table A4).

Table 1 Populations of the Common Redstart *Phoenicurus phoenicurus* included in the study

ID	Co-author/s	Biotope characteristics	Country	Area (near town)	Coordinates	Period	Years	Broods	Laying dates (means of the season values ± SE)			Second broods
									<i>n</i>	<i>n</i>	Minimum	
1	Mertens and Sombrutzki	Germany	Stuttgart	48°31'N 09°19'E	1987–2009	17	204	–2.47 ± 0.95 <i>T</i> _{min} = 11.95 ± 0.91 °C	6.59 ± 1.67	41.47 ± 1.71	Yes	
	Old, high-stemmed orchards, altitude 263–430 m											
2	Porkert and Zajić	Czech Rep.	Hradec Králové	50°10'N 15°57'E	1986–2010	19	316	3.11 ± 0.72 <i>T</i> _{min} = 14.05 ± 0.79 °C	17.66 ± 1.82	45.37 ± 2.26	Yes	
	Scots pine <i>Pinus sylvestris</i> forest, altitude 300 m											
3	Numerov	Russia	Oksky Nature Reserve	54°53'N 40°50'E	1975–1989	11	124	14.81 ± 1.39 <i>T</i> _{min} = 14.07 ± 1.32 °C	25.45 ± 1.75	43.36 ± 3.01	Yes	
	Scots pine <i>Pinus sylvestris</i> or mixed forests, altitude 80–160 m											
4	Belskii	Russia	Revda	56°51'N 59°53'E	1992–2010	19	410	19.21 ± 1.10 <i>T</i> _{min} = 10.64 ± 1.13 °C	31.13 ± 0.95	54.26 ± 2.08	Yes	
	Rarefied mixed forests (<i>Betula</i> , <i>Populus</i> , <i>Picea</i> , <i>Abies</i> , <i>Pinus</i>) near an industrial site, altitude 360–430 m											
5	Kuranov and Gashkov	Russia	Tomsk	84°54'E	1986–2009	20	422	16.65 ± 0.77 <i>T</i> _{min} = 11.62 ± 1.25 °C	24.58 ± 0.72	47.95 ± 2.45	No	
	Tomsk town parks and nearby mixed forests, mainly broad-leaved, altitude 130–140 m											
6	Ruttila and Haikola	Finland	S. Karelia	61°26'N 28°14'E	1983–2010	28	1,116	17.64 ± 0.77 <i>T</i> _{min} = 10.20 ± 0.74 °C	29.73 ± 0.84	54.11 ± 1.80	(Yes)	
	Scots pine <i>Pinus sylvestris</i> forest, altitude 100 m											
7	Lajta	Finland	Joensuu	63°05'N 30°35'E	1987–2010	23	829	19.39 ± 1.03 <i>T</i> _{min} = 9.00 ± 0.99 °C	30.83 ± 0.76	58.48 ± 0.94	(Yes)	
	Scots pine <i>Pinus sylvestris</i> forest, altitude 100–170 m											
8	Jokimäki, Huhta and Jokimäki	Finland	Rovaniemi	66°30'N 25°44'E	1992–2010	10	201	21.20 ± 1.78 <i>T</i> _{min} = 7.63 ± 1.24 °C	28.90 ± 1.71	39.30 ± 2.27	No	
	Scots pine <i>Pinus sylvestris</i> forest, altitude 200 m											
9	Järvinen	Finland	Kilpisjärvi	69°03'N 20°50'E	1969–2008	34	460	30.50 ± 0.69 <i>T</i> _{min} = 4.65 ± 0.55 °C	36.72 ± 0.80	47.29 ± 1.03	No	
	Mountain birch <i>Betula pubescens</i> forest, altitude 475–600 m											

The first-egg laying dates in the table are the number of days before/after 30 April (e.g. –2 = 28 April, 1 = 1 May, 32 = 1 June). The rare occurrence of second broods is indicated by parentheses

ID identification number of a population used in the study, *T*_{min} mean air temperature at the mean minimum laying date over the period

The effects of large-scale climatic patterns were tested by the use of northern hemisphere indices: NAO, East Atlantic pattern (EA), and Scandinavia/Eurasia-1 pattern (SCAND). While positive NAO and EA are associated with warm temperatures in western and central Europe, positive SCAND is associated with the opposite effect (<http://www.cpc.ncep.noaa.gov/data/teledoc/telecontents>). All indices were used as means over the months December–March.

Analyses

We computed overall means over the years of observation of all broods in each population. These were the means of minimum, median, and maximum first-egg laying, range of laying dates per season, and the air temperature at mean minimum first-egg laying dates (T_{\min}). We tested the effects of geographical latitude, longitude, and mean altitude of the populations on the above variables by three-way ANOVA. Further, we correlated latitude, longitude, and altitude separately to the above population variables using Pearson correlation coefficients. The variables followed normal distribution (Shapiro–Wilk test, $p > 0.16$). We plotted the mean air temperature (T_{\min}) in relation to the latitude of each population (Fig. 3).

In the second part of the analyses, we used the minimum (Min) and the median (Med) first-egg laying dates

after exclusion of those breeding attempts that were not truly the first (see above) in each year as the laying date variables. We computed simple linear regressions to test the trends of the laying dates over the years of the study and the effects of weather (local air temperature, large-scale climatic patterns). The slopes of the regression of laying dates and air temperature against the year of observation were displayed together in x - y plots (Fig. 4a, b). We correlated the number of the started broods in a day with the mean temperature over the previous three, five, and 10 days to test the instant effect of temperature on the initiation of egg laying (under the assumption of independency of the start of each brood). The Spearman correlation coefficients of the observed years were averaged for each population.

We used a general linear mixed model (Proc Mixed, SAS Institute 2000) to analyze the effects of year, temperature, geographical latitude, and longitude on the start of breeding season (minimum and median) across the populations. In the test, we merged data of the seven populations with the most complete time series from the year interval 1986–2010 (population ID 1, 2, 4, 5, 6, 7, 9b). The population identity entered the model as a random factor. The effect of mean altitude was insignificant and the variable was excluded.



Fig. 1 Locations of Common Restarct *Phoenicurus phoenicurus* populations included in the study. The numbers in the picture correspond to ID in Table 1

Results

The laying period of the Common Redstart varied between different populations. The breeding season in the southernmost population (ID 1—southern Germany) started about one month earlier than in the northernmost population (ID 9—northern Finland, Table 1; Fig. 2a–i). The three-way analysis of variance (ANOVA) test showed a distinct effect of latitude on all the means of minimum and median first-egg laying dates, air temperature at minimum first-egg laying date (T_{min}), and the range of laying dates per season. The effects of longitude and altitude were unclear (Online resource Table A2).

A correlation analysis revealed a strong positive correlation between the means of annual population laying dates and latitude (Pearson correlation: $r = 0.92$, $n = 9$, $p = 0.0004$ for minimum laying dates, $r = 0.86$, $n = 9$, $p = 0.0029$ for median laying dates). There was a relationship between the temperature at minimum laying date (T_{min}) and the latitude of a population ($r = -0.89$, $n = 9$, $p = 0.0013$) that was consistent with the relation of latitude and the length of photoperiod at minimum laying date (Fig. 3). This indicates that the populations in the north, despite their much later start, breed in lower temperature conditions, and the start is connected to photoperiod. There

Fig. 2 Seasonal distribution of broods (first-egg laying dates) of individual populations summarized across years with six or more observed broods. The numbers in the x-axis represent the pentades of the spring months (e.g. -1 represent the last five days of April, 1 is the first five days of May, etc.). The brood numbers documented on 31 May were evenly divided between pentades 6 and 7. The open bars represent first broods, solid bars second broods and hatched bars replacement broods. In some populations, second and/or replacement broods were not documented, and all broods together (wide open bars) are displayed in a graph. The ID numbers in the graphs correspond to the IDs in Table 1

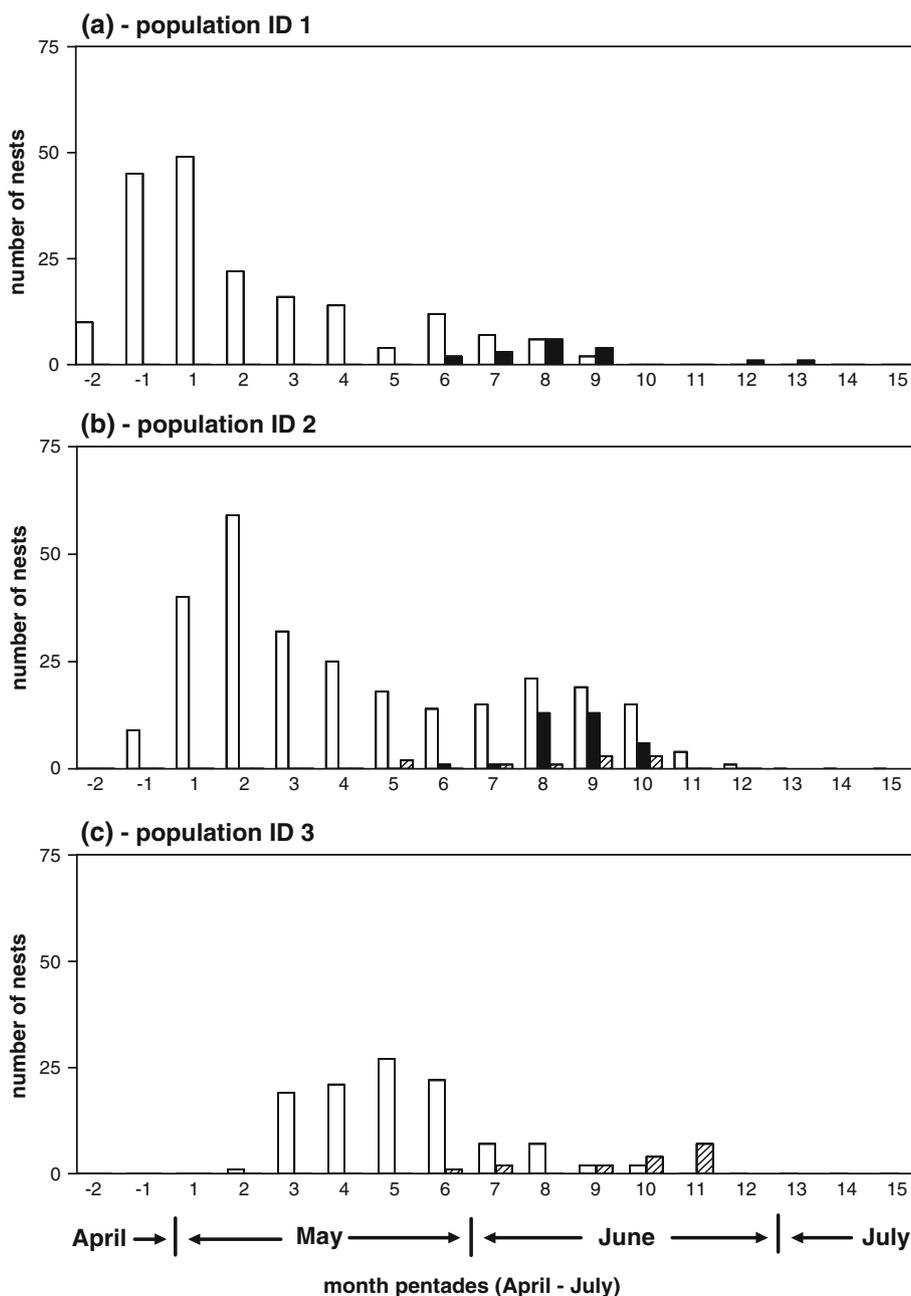
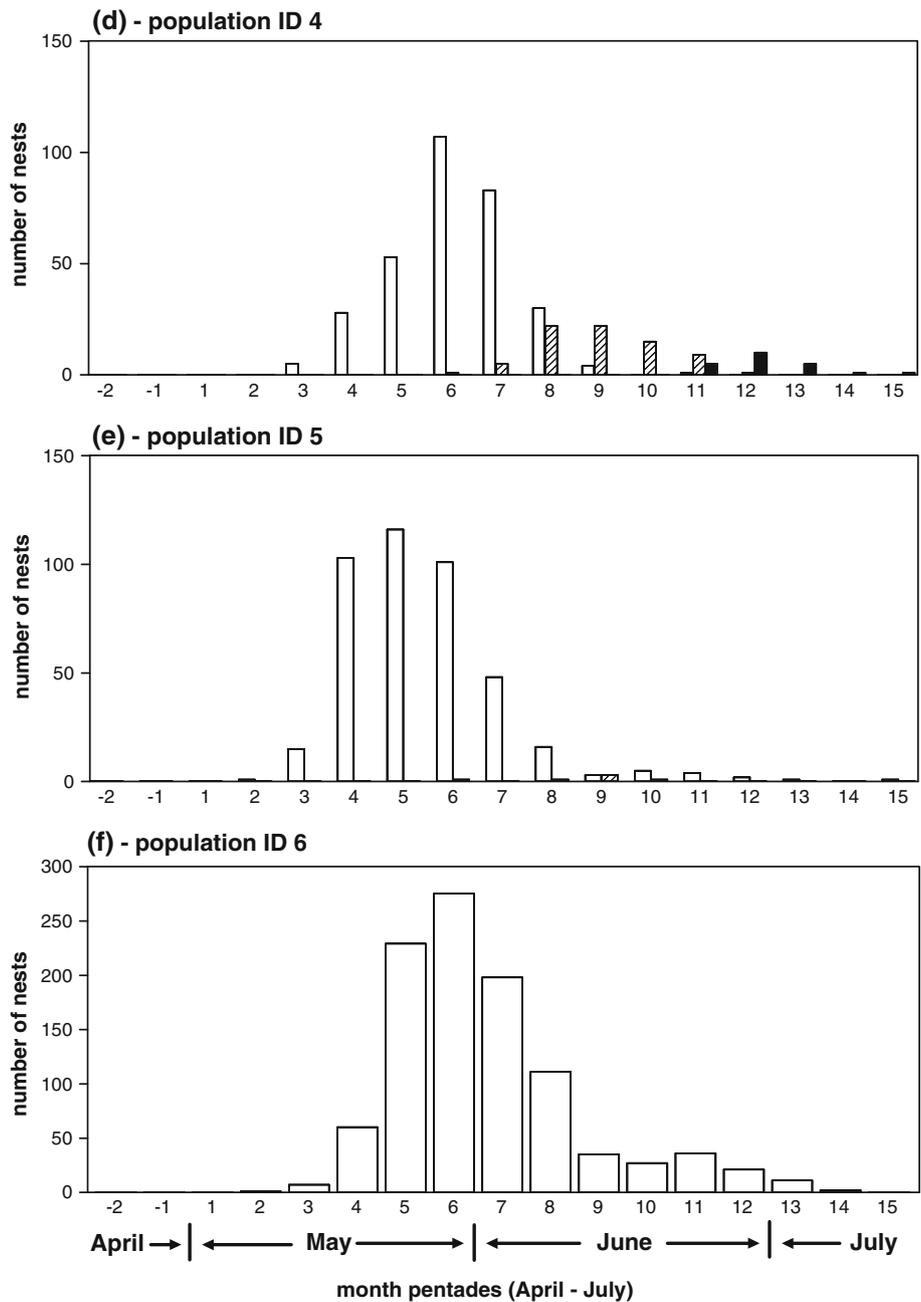


Fig. 2 continued



was no significant correlation of longitude or altitude with any tested variables ($p > 0.45$, $p > 0.25$, respectively).

The true second broods occurred mostly in populations located in the southern part of the studied distribution area, but there was a rare occurrence of second broods in two Finnish populations too (ID 6, 7). The length of the laying period measured as the range between maximum and minimum laying date correlated significantly with the latitude ($r = -0.77$, $n = 9$, $p = 0.0147$) but not with the longitude or altitude ($r = -0.11$, $n = 9$, $p = 0.7854$, $r = -0.21$, $n = 9$, $p = 0.5910$, respectively). The mean maximum laying date range was 43.9 days in the

population ID 1 and minimum range 16.8 days in the population ID 9.

The yearly effect on the first-egg laying date was negative in most populations/intervals (Table 2), although it was statistically significant only in three populations. The effect was positive or negligible in two Russian populations (ID 4, 5). A negative effect means that the start of the laying period advances over the years of observation. Following this definition, the effect of air temperature on the date of egg laying was strongly negative and significant in most populations/intervals. The means of local air temperature tended to increase over the years (except in

Fig. 2 continued

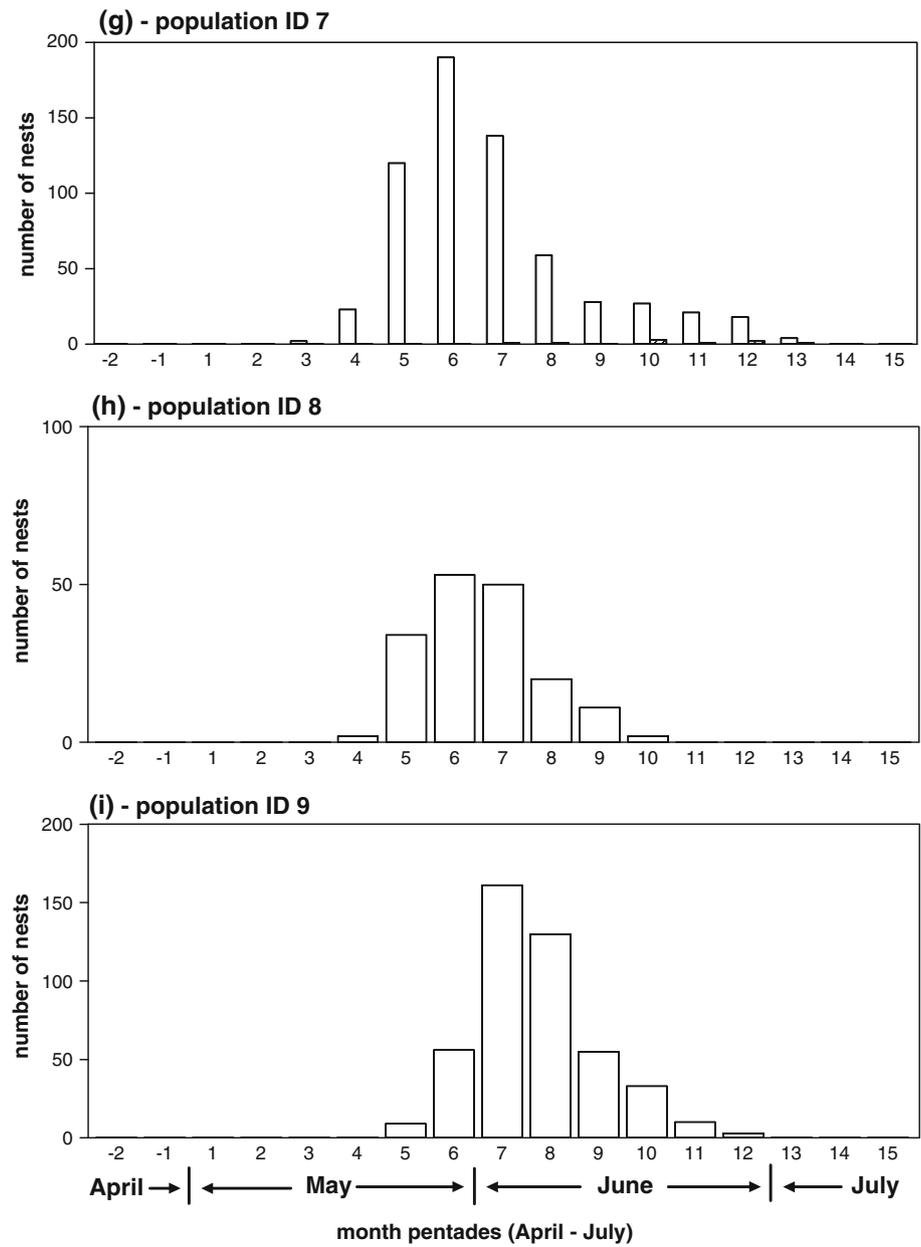
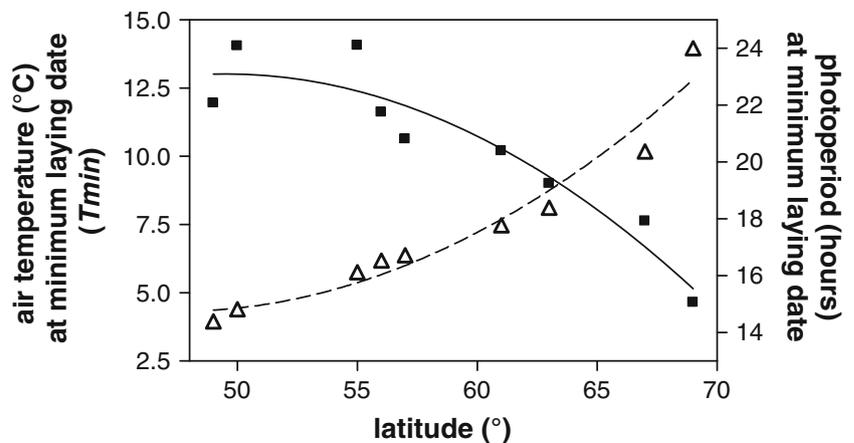


Fig. 3 Mean air temperatures (T_{\min}) (full squares, solid line) and length of photoperiod (open triangles, hatched line) at the mean minimum first-egg laying dates in relation to the latitude of the observed populations. The lines are fits from quadratic regressions, $R^2 = 0.89$ resp. 0.9512



populations ID 3 and ID 6), but a statistical significance was reached in one population only. There was no obvious relation between a greater temperature change and a greater advance of egg laying over the period, and vice versa (Fig. 4a, b).

The large-scale climatic patterns (NAO, EA, SCAND) had a low effect on the minimum and median dates of the start of redstart breeding season (Online resource Table A3).

A correlation analysis of the number of started broods in a day did not reveal short-term effects of the temperature, although mean temperature correlations of the previous three and five days before the starts were mostly positive (Online resource Table A4).

The mixed model of the joined populations (ID 1, 2, 4, 5, 6, 7, 9b) of the year interval 1986–2010 (Table 3) documented significant effects of the local air temperature and geographical latitude on the minimum and median first-egg laying dates. The minimums and medians of the start of redstart laying periods occurred earlier in higher spring air temperatures (1.15 and 1.31 days/°C, respectively) and later in higher latitudes (1.04 and 1.03 days/°, respectively). The effect of geographical longitude was rather positive but not significant. The start of a laying period tended to be earlier, but was significant in median first-egg laying dates only. The median dates advanced for 0.11 days/year over the 25-year period.

Discussion

Departure from a wintering area, migration route, and speed or arrival in the breeding area in migratory birds may be influenced by large-scale effects and climate. In contrast to arrival dates, registration of the start of breeding provides an accurate representation of the reproduction strategy of the individuals in a local population, which is rather dependent on local weather and ecological conditions (Both et al. 2004). In our study, we documented great differences in the start and distribution of broods during a season, especially along the north–south gradient. There was a strong negative effect of local air temperatures on the egg laying dates across the studied populations, but the long-term change was rather weak and variable, although negative in most cases.

As shown by our data, the egg laying starts about one month later in the northern Europe (late May/start of June) than in the central European populations (end of April/start of May). Further to the south, in northern African, Mediterranean, and western Asian arid zones, the advancement of the redstart breeding season to earlier spring dates is probably limited by a shift of the preferred redstart breeding habitat to higher altitudes. The redstart breeding habitat in Morocco is situated at altitudes between 1,500

and 2,200 m, and the breeding starts in the first half of May (Thévenot et al. 2003). At the altitudes over 1,000 m in Armenia, the laying occurs at the beginning of May with a minimum extreme on 26 April (Adamian et al. 1999). In a subalpine zone of Tien-Shan/Kazakhstan, nests occur at altitudes 1,900–2,700 m, and the egg laying starts in a majority of nests as late as in the first and second weeks of June (Kovshar 1979). We did not find a significant effect of altitude on the start of the laying period in our study, probably due to small differences in altitude between the tested population areas.

Our data have shown a close connection between local air temperature and the start of breeding. The effect of large-scale climatic patterns was weak. This is in contrast with studies of migration where NAO has a strong effect (e.g. Hüppop and Hüppop 2003). The timing of breeding depends more on local conditions (e.g. Ahola et al. 2004; Sokolov 2006; Rubolini et al. 2007; Hušek and Adamík 2008; Dyrzc and Halupka 2009; Potti 2009; Bauer et al. 2010), although it may be influenced by previous effects already in the wintering area (McKellar et al. 2013). The onset of egg laying may be more attuned to environmental conditions than to the concentration of gonadotrophic hormones or gonadal growth, as documented in studies of the Great Tit (*Parus major*) (Schaper et al. 2012). In a detailed study of the Collared Flycatcher (*Ficedula albicollis*) (Weidinger and Král 2007), the number of initiated clutches was most associated with the daily temperature three days before the initiation. We could not confirm the short-term temperature effect in our study, however, mean correlations of the temperature from a three-day period and the number of consequently started broods were mostly positive. The differences of the mean temperature at the onset of laying between populations of different latitudes (Fig. 3) were probably caused by their responses to photoperiod. The reaction to photoperiodicity is probably genetically fixed and overrides environmental or physiological factors in the start of laying (Lambrechts et al. 1997; Lambrechts and Perret 2000). Long-term shifts in the timing of reproduction independent of temperature fluctuations thus may indicate micro-evolutionary change in a population.

There has been a widespread advancement of the spring passage and arrival time of most migrating bird species in the western Palearctic over the past decades (Lehikoinen et al. 2004; Sparks et al. 2007; Sokolov 2006; Hüppop and Hüppop 2003). However, the timing and speed of migration depends on weather effects on the route, especially in long-distance migrants (Ahola et al. 2004; Zalakevicius et al. 2006; Hüppop and Winkel 2006; Tøttrup et al. 2008; Halkka et al. 2011). In the Common Redstart, the spring migration and arrival has advanced over the second half of the twentieth century at most observation points in western and eastern Europe: England (Croxtton et al. 2006; Sparks

Table 2 Results of simple linear regression analyses of the effects of year or local air temperature (Temp) on the first-egg laying dates (Min, Med), and the effect of year on local air temperatures (Temp)

ID	Country	Min: year			Med: year			Temp: year		
		Slope (SE)	$F(df)$ p	Slope (SE)	$F(df)$ p	Slope (SE)	$F(df)$ p	Slope (SE)	$F(df)$ p	
1	GER	-0.0757 (0.1548)	$F(1,15) = 0.24$ $p = 0.6361$	-1.9043 (0.5965)	$F(1,15) = 10.19$ $p = 0.0061$	-0.2321 (0.2021)	$F(1,15) = 1.32$ $p = 0.2689$	0.1042 (0.0473)	$F(1,15) = 2.88$ $p = 0.1106$	$F(1,21) = 4.85$ $p = 0.0390$
2	CZE	-0.2400 (0.0822)	$F(1,17) = 8.52$ $p = 0.0096$	-0.8595 (0.2871)	$F(1,17) = 8.96$ $p = 0.0082$	-0.2679 (0.1897)	$F(1,17) = 1.99$ $p = 0.1759$	0.0547 (0.0548)	$F(1,17) = 11.59$ $p = 0.0034$	$F(1,23) = 0.99$ $p = 0.3293$
3	RUS	-0.3486 (0.3020)	$F(1,19) = 1.33$ $p = 0.2782$	-1.7672 (0.2752)	$F(1,19) = 41.24$ $p = 0.0002$	-0.2004 (0.4191)	$F(1,9) = 0.23$ $p = 0.6439$	0.0004 (0.1602)	$F(1,8) = 6.09$ $p = 0.0388$	$F(1,12) = 0.00$ $p = 0.9981$
4	RUS	0.1561 (0.2035)	$F(1,17) = 0.59$ $p = 0.4534$	-1.2782 (0.5801)	$F(1,17) = 4.86$ $p = 0.0416$	-0.0886 (0.1926)	$F(1,17) = 0.21$ $p = 0.6514$	0.1162 (0.0709)	$F(1,17) = 9.92$ $p = 0.0059$	$F(1,17) = 2.69$ $p = 0.1196$
5	RUS	-0.0142 (0.1108)	$F(1,18) = 0.02$ $p = 0.8998$	-0.9431 (0.2891)	$F(1,18) = 10.64$ $p = 0.0043$	-0.0493 (0.0984)	$F(1,18) = 0.25$ $p = 0.6227$	0.0538 (0.0662)	$F(1,18) = 12.61$ $p = 0.0023$	$F(1,22) = 0.66$ $p = 0.4254$
6	FIN	-0.0591 (0.0958)	$F(1,26) = 0.38$ $p = 0.5426$	-1.0178 (0.4680)	$F(1,26) = 4.73$ $p = 0.0389$	-0.1633 (0.0959)	$F(1,26) = 2.90$ $p = 0.1005$	-0.0221 (0.0369)	$F(1,26) = 2.78$ $p = 0.1074$	$F(1,26) = 0.36$ $p = 0.5542$
7	FIN	-0.3147 (0.1340)	$F(1,21) = 5.52$ $p = 0.0287$	-1.5064 (0.6242)	$F(1,21) = 5.82$ $p = 0.0250$	-0.2077 (0.1145)	$F(1,21) = 3.29$ $p = 0.0840$	0.0745 (0.0440)	$F(1,21) = 3.80$ $p = 0.0648$	$F(1,22) = 2.87$ $p = 0.1045$
8	FIN	-0.2873 (0.2792)	$F(1,8) = 1.06$ $p = 0.3335$	-2.6916 (0.8295)	$F(1,8) = 10.53$ $p = 0.0118$	-0.4844 (0.2289)	$F(1,8) = 4.48$ $p = 0.0672$	0.1007 (0.0605)	$F(1,8) = 21.51$ $p = 0.0017$	$F(1,17) = 2.77$ $p = 0.1141$
9a	FIN	-0.3390 (0.1430)	$F(1,9) = 5.62$ $p = 0.0419$	-1.7404 (0.3534)	$F(1,9) = 24.25$ $p = 0.0008$	-0.3954 (0.1945)	$F(1,9) = 4.13$ $p = 0.0726$	0.1178 (0.0683)	$F(1,9) = 12.65$ $p = 0.0061$	$F(1,14) = 2.98$ $p = 0.1065$
9b	FIN	-0.1828 (0.1382)	$F(1,21) = 1.75$ $p = 0.2002$	-2.4661 (0.7008)	$F(1,21) = 12.38$ $p = 0.0020$	-0.1962 (0.1574)	$F(1,21) = 1.55$ $p = 0.2264$	0.0396 (0.0345)	$F(1,21) = 14.36$ $p = 0.0011$	$F(1,21) = 1.32$ $p = 0.2633$

ID numbers of populations as in Table 1

Table 3 Mixed-model analyses with *minimum first-egg laying date* (a) and *median first-egg laying date* (b) as dependent variables ($n = 146$ season values)

Variable	Estimate \pm SE	$F(df)$	p
(a) Minimum first-egg laying date			
Fixed effects			
Year	-0.07 ± 0.05	$F(1,137) = 2.60$	0.1094
Air temperature	-1.15 ± 0.18	$F(1,138) = 40.03$	<0.0001
Latitude	1.04 ± 0.21	$F(1,4.47) = 25.61$	0.0053
Longitude	0.12 ± 0.05	$F(1,3.8) = 5.54$	0.0816
Random effect			
Population	11.50 ± 8.84		
Residual	12.86 ± 1.55		
(b) Median first-egg laying date			
Fixed effects			
Year	-0.11 ± 0.05	$F(1,137) = 5.17$	0.0245
Air temperature	-1.31 ± 0.20	$F(1,141) = 43.85$	<0.0001
Latitude	1.03 ± 0.35	$F(1,4.15) = 8.96$	0.0383
Longitude	0.15 ± 0.09	$F(1,3.88) = 2.82$	0.1705
Random effect			
Population	35.37 ± 25.97		
Residual	14.89 ± 1.80		

The fixed effects are year, local air temperature, and geographical latitude and longitude of a population. The random effect is the identity of the studied population. The statistical analysis includes data from years 1986–2010 of the seven populations with the most complete time series (mean number of years per population \pm SD = 20.86 ± 2.85). Estimates in the table are slopes \pm SE of fixed effects and covariance parameter \pm SE of random effects. The F and p values are of the type 3 tests of the fixed effects. The effective degrees of freedom in the tests were calculated by Satterthwaite's estimation (Proc Mixed, SAS Institute 2000)

et al. 2007), Scotland (Jenkins and Watson 2000), Helgoland/northern Germany (Hüppop and Hüppop 2003), and Vilnius/Lithuania (Zalakevicius et al. 2006). In contrast, negligible or no change over the period is documented from Ottenby/southeastern Sweden (Stervander et al. 2005) and the Courland Spit in the Baltic Sea/western Russia (Sokolov 2006). It is expected that the populations of eastern Europe or the populations using southeastern paths for migration would change less on a long-term scale than the populations of the western migration routes that are more affected by oceanic weather (Hüppop and Hüppop 2003). However, the above list of results does not show such correlation clearly. This may be the result of local weather deviations or of the few data available to represent the geographic variability of the species behavior. In our study, the change of the start of breeding seasons differed between the studied populations of different geographical regions. While the laying dates advanced markedly in most Fennoscandian populations and the population in Czech Republic (ID 2), there were slight opposite or negligible

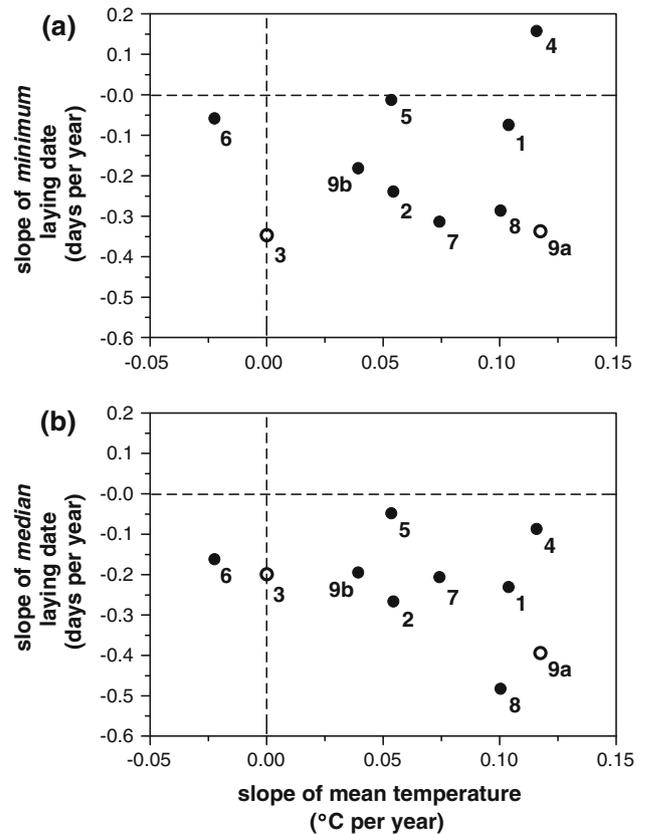


Fig. 4 The slopes of minimum laying date (a) and median laying date (b) over the years of observation in relation to the local temperature trends. The numbers in the plots correspond to IDs in Table 1. The population ID 9 was split into two-year periods (9a and 9b), as in Table 2. The open circles represent populations and year periods not matching the majority data following the year 1986 (filled circles)

changes in the populations in Ural or western Siberia (ID 4, 5) that may reflect their more eastern migration routes.

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