

The breeding biology of the common redstart, *Phoenicurus phoenicurus*, in the Central European pine forest

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Received 22 June 2004; Accepted 9 May 2005

Abstract. The breeding biology of the common redstart, *Phoenicurus phoenicurus*, was studied from 295 nests over 20 years in a nest-box population breeding in managed pine forest in the northeast of the Czech Republic, central Europe. The laying of first eggs lasted from 30 April until 30 June with two distinct peaks in May and June. The estimated proportion of pairs producing two broods per season was 65.4%, the highest estimate in studies of this species. Nest success was only 45.1%, one of the lowest known values. The mean clutch size was 6.30 eggs in assumed first broods and 5.39 eggs in assumed second broods. The production of two broods per season and relatively small clutches is probably a parental adaptation to conditions of frequent nest predation. The two breeding attempts per season could not, however, compensate for the latitudinal differences in clutch size and breeding success, and the seasonal breeding productivity was lower in comparison to populations in the northern area of distribution. At higher air temperatures the breeding started earlier. The air temperature also affected nest success which was highest at mean temperature values and decreased to both low and high temperature extremes. The effects of precipitation, first-egg-laying date, clutch size and year of observation on nest success were not significant.

Key words: egg laying, clutch size, hatching, fledging, nest success, altricial birds

Introduction

The common redstart, *Phoenicurus phoenicurus*, is a hole-nesting passerine with a large latitudinal range in breeding distribution (Cramp 1988, Glutz von Blotzheim et al. 1988, Hagemeyer & Blair 1997). A large variability has been documented in breeding performance of this species between populations along the north-south gradient. In the north, the mean clutch size is larger, breeding starts later and lasts for a shorter period, while the overall nest success is higher (Järvinen 1978, Pulliainen et al. 1982, Vestola et al. 1996) than in populations from central Europe (Blát 1976, Winkel 1986). Some pairs are able to raise two broods per season but only in populations from the central and southern distribution area (Menzel 1984).

This study presents data from 20 years of observation of the redstart breeding population from a pine forest in the northeast of Czech Republic, at the centre of distribution range. We estimated the proportion of pairs raising two broods per season and compared the differences in clutch size and the success of hatching and fledging between first and second broods. We also tested the effects of weather on the onset of breeding and examined factors influencing the proportion of nests surviving to fledging.

Common redstart populations have declined throughout the Europe since about the middle of the last century (Bernadt & Winkel 1979, Järvinen 1981, Hagemeyer &

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Blair 1997). We tested whether the timing and success of breeding had changed over the 20 years of our study to see if they might have contributed to population changes.

Material and Methods

Study area and data collection

The data set contains results of 295 breeding attempts of common redstarts in nest-boxes east of the town Hradec Králové, 50°12'N, 15°57'E, Czech Republic, in 20 breeding seasons in the years 1983–2002.

The study area was a managed pine *Pinus sylvestris* forest (forest type *Querceto-Pinetum*), lacking shrub layer and with a ground cover of bilberries *Vaccinium myrtillus*. The study area was about 10 km² large, in a flat landscape at altitude 250 m. It was part of a large forest complex extending for about 50 km along the river Orlice in the agricultural land of eastern Bohemia. The mean air temperature over the observed seasons (n = 20 years) was 9.10°C in April (SD = 1.46), 14.68°C in May (SD = 1.71), 16.97°C in June (SD = 1.47) and 19.03°C in July (SD = 1.85), and the mean month sum of precipitation was 38.56 mm (SD = 16.45), 57.60 mm (SD = 34.65), 67.24 mm (SD = 27.08) and 87.66 mm (SD = 49.80), respectively (Czech Hydrometeorological Institute). There was no clear trend in air temperature or precipitation over the 20 year period of observation.

There were about 350 nestboxes (10 x 10 x 22 cm of inner dimensions, entrance hole diameter 32 mm) in the study area, placed in lines at a distance of 30–50 m apart, attached at 3 m height to the tree trunk.

On average 15 nests (3 to 34 nests) were observed each season and the observations were made from late April to mid-July. In four years, the observation through season was not continuous and the number of the observed nests was small, so data of these nests were not included in the analysis of timing of egg-laying or the effect of year. Nests were visited usually once every five days but the frequency of visits to some broods and periods was higher. Due to lack of some data from some nests (e.g., observation discontinuity), different numbers of nests were used in the statistical analyses.

Data analysis

General assumptions

As there were several days gaps between visits to nests, some aspects of the breeding cycle were not observed directly. For the calculation of egg-laying dates, clutch size and age of broods, we therefore used several assumptions of breeding biology taken from literature (e.g. Menzel 1984, Cramp 1988, Glutz von Blotzheim et al. 1988); these were also confirmed by our own partial observations. The assumptions were: 1. females lay one egg per day; 2. females begin incubation after laying the last egg; 3. incubation of the clutch averages 14 days; 4. we determined the exact age of chicks according to their body and sensory development up to age 10 days (hatching = day 0).

All chicks of a brood usually fledged together during one or two days at an average age of 13 days (Buxton 1950, Menzel 1984). As the disturbance of older chicks may initiate fledging, we checked nests for the last time at age 10 days. We assumed the breeding attempt was successful when chicks reached the age of ten days, appeared in good condition and the

nest was intact. As ten day old chicks are fully feathered, reach or exceed the body weight of adults, and are able to fly, we assume they are able to survive even outside the nest.

Determination of first and second broods

In our study we did not focus specifically determining first and second broods; however, we observed two broods per season in 24 breeding pairs by casual ringing recoveries or by observing the building of a second nest while still feeding the first brood. As these first and second breeding attempts corresponded to the peaks of laying of all observed nests, but did not coincide with each other (Fig. 1), we divided all studied nests into two groups according to their laying dates. We assumed nests were ‘first’ broods where laying of eggs started in April or May and as the ‘second’ broods where laying started in June. Both, ‘first’ and ‘second’ brood groups contain an unknown proportion of replacement breeding attempts. However, since the probability of nest failure does not differ significantly between incubation and nestling periods and there is also no statistical difference in the nest success between both ‘first’ and ‘second’ brood groups (see Results), we assume replacement nesting attempts occur at a constant rate throughout the whole breeding period (except at the end of season). Thus the proportion of replacement broods on the overall number of breeding attempts should not misrepresent the distribution curve of first and second broods. Replacement breeding usually starts immediately after the failure of the previous brood, on the next or even the same day (Menzel 1984).

Specification of variables

The egg-laying date was back-calculated using the above general assumptions. Clutch size was calculated when incubation was underway. Hatching success was calculated from the period between first egg and hatching (which was assumed to be finished two days after the first chick had hatched). Hatching was highly synchronous as the egg incubation in common redstart starts after the last egg of a clutch is laid (Menzel 1984). Hatching success was assessed as three variables: (a) total nest failure binary variable: no eggs hatched vs. one or

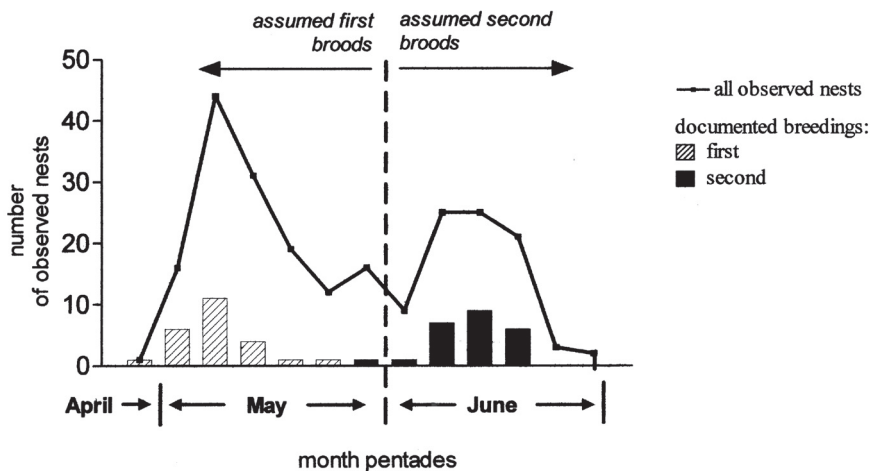


Fig. 1. Seasonal distribution of dates of first eggs in month pentades, (n = 224 nests). Replacement broods are included in the overall nest numbers.

more eggs hatched; (b) full/partial hatching binary variable: all eggs hatched vs. part of the brood failed to hatch; (c) mean hatching success and the number of eggs failed to hatch per nest of the partially hatched nests, i.e. of the nests where part of the brood failed to hatch.

Several nests were deserted or destroyed in the interval between two nest visits at around the predicted time of hatching; such nests were omitted from calculations of either hatching or fledging successes, but were included in the overall nest success.

Fledging success was calculated as three variables from the period between hatching until fledging (chick age of ten days – see General assumptions), i.e. from a data set independent of the nests from previous egg-incubation interval: (a) total nest failure binary variable: no chicks fledged vs. one or more chicks fledged; (b) full/partial fledging binary variable: all chicks fledged vs. part of the brood failed to fledge; (c) mean fledging success and the number of chicks which failed to fledge per nest of the partially fledged nests.

The overall nest success was calculated by multiplying the values of hatching and fledging successes (unknown nest failures included) because the numbers of nests observed in egg and nestling intervals were different due to incomplete observation period in some nests. We further calculated mean number of chicks fledged per successful nest.

Statistics

Differences in clutch size and number of fledged chicks between ‘first’ and ‘second’ broods were tested by two-sample t-test. Differences between hatching success in ‘first’ and ‘second’ broods were tested by Fisher’s exact test (binary variables) and by two-sample t-test (mean hatching success). Similar tests were used for comparison of ‘first’ and ‘second’ broods’ fledging success. The difference in success between periods of hatching and fledging (hatching and fledging success binary variables) was also tested by Fisher’s test.

The effects of weather (sum of precipitation and mean air temperature in the last ten days of April) and year of observation on the start of breeding (median of ‘first’ broods’ first-egg-laying dates, day 0 = 30 April) were examined by regression. Specifically, a multiple linear regression with backward elimination for the selection of explanatory variables was computed (SAS Institute 2000).

A multiple logistic regression model with backward elimination (SAS Institute 2000) was used to test the dependence of overall nest success on the effects of first-egg-laying date, number of eggs in a clutch, sum of precipitation and mean air temperature of the interval of 28 days since clutch was completed, and year of observation. As we assume the effects of independent variables may not be linear, i.e. nest success may be optimal at medium values of an independent variable, all effects except the year of observation were included in the model as both linear and squared terms. The tested data set was restricted to the nests continually observed since egg-laying. A significance level for elimination of variables from a model was $P = 0.1$ in both regression models.

Results

Egg-laying and proportion of second broods

The egg-laying period lasted through May and June with two distinct peaks, in the second pentad of May and the second to third pentad of June (Fig. 1). The earliest observed date of first egg was 30 April and the latest was 30 June ($n = 224$ nests). When the broods were

Table 1. Effects of weather in last April decade and year of observation (treated as continuous) on the median first-egg-laying date of the ‘first’ broods. Independent variables in the final model of multiple regression were selected by backward elimination at the significance level of $P = 0.1$. Data in the table are from a common redstart nest-box population from the northeast of Czech Republic, observed between years 1983–2002, ($n = 16$ years).

	Parameter estimate	SE	t	P
Null model				
Intercept				NS
Sum of precipitation				NS
Mean air temperature				< 0.05
Year of observation				NS
Final model				
Intercept	-21.30	4.17	5.11	< 0.001
Mean air temperature	-0.77	0.33	-2.34	0.035

divided (see Methods) into ‘first’ broods (those with egg-laying starting in April or May) and ‘second’ broods (egg-laying starting in June), the laying of second broods occurred in 65.4 % of the nests which had started in April and May. The median date of egg-laying for ‘first’ broods was May 12 ($n = 139$ nests) and for ‘second’ broods was June 12 ($n = 85$ nests). The timing of the two broods in a season was documented in 24 individually observed breeding pairs. The mean time gap for the laying of first eggs between first and second broods was 35.9 days ($SD = 4.7$, range 29–44 days).

The median date for the laying of first eggs was significantly affected by the mean air temperature in the last ten days of April. The sum of precipitation and year were eliminated from the final regression model (Table 1). At higher temperatures, breeding started earlier (Fig. 2).

Clutch size

The number of eggs in a clutch fluctuated throughout season but generally decreased with an increase in the date of first egg (Fig. 3). This was confirmed by a comparison of assumed

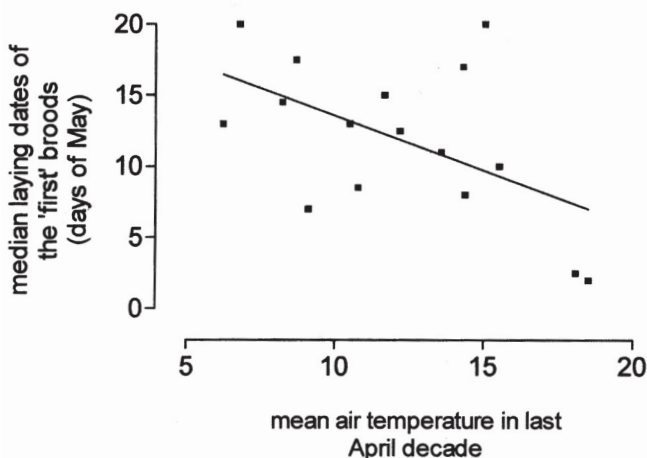


Fig. 2. Relation between mean air temperature in last April decade and seasonal medians of date of first eggs of ‘first’ broods, ($n = 16$ years). The line represents the predicted values of regression model (Table 1).

‘first’ and ‘second’ broods. The mean clutch size in the ‘first’ broods was 6.30 eggs (SD = 0.88, n = 100 nests) and in the ‘second’ broods 5.39 eggs (SD = 0.94, n = 72 nests) and the difference was significant ($t = 6.49$, $df = 170$, $P < 0.001$). The number of eggs in a clutch ranged from three to eight eggs. The most frequent clutch size was seven eggs in the ‘first’ broods and five eggs in the ‘second’ broods. The clutch size in both groups may be biased by an unknown proportion of replacement clutches.

Hatching success

Some 26% of nests with eggs failed to hatch at all (Table 2). Hatching failure was caused by nest desertion (60%) or predation/damage of the whole clutch (40%). Of the remainder, all eggs hatched in more than 50% of cases (Table 2). The difference between ‘first’ and ‘second’ broods was not significant in any of the tested hatching variables.

In addition to 210 nests of known hatching success, 17 nests failed in the interval between two nest visits at the time of supposed hatching. Combining these, 31.7% of observed clutches failed.

Fledging success

In 34% of clutches which hatched, no chick survived to fledging (Table 3). Total fledging failures were caused by desertion (14.7%) or predation (85.3%). Of the remainder, all young

Table 2. Hatching success of common redstart broods calculated from the period between first-egg-laying and hatching: (a) total nest failure binary variable: no eggs hatched vs. one or more eggs hatched; (b) full/partial hatching binary variable: all eggs hatched vs. part of the brood failed to hatch; (c) mean hatching success and the number of eggs failed to hatch per nest of the partially hatched nests. Data in the table are from a nest-box population from the northeast of Czech Republic, observed in years 1983–2002.

	All nests	‘First’ broods	‘Second’ broods	‘First’ - ‘Second’ broods comparison
(a)				
Number of observed nests	210	125	85	
Proportion of hatched nests	0.74	0.70	0.80	Fisher’s exact test $P = 0.110$
(b)				
Number of hatched nests	155	87	68	
Proportion of partially hatched nests	0.42	0.45	0.38	Fisher’s exact test $P = 0.509$
(c)				
Hatching success of partially hatched nests (mean \pm sd)				
hatching success per nest	0.72 \pm 0.17	0.73 \pm 0.18	0.71 \pm 0.15	$t_{63} = 0.31$ $P = 0.756$
total number of eggs lost per nest	1.59 \pm 0.99	1.66 \pm 1.07	1.50 \pm 0.86	$t_{63} = 0.63$ $P = 0.534$

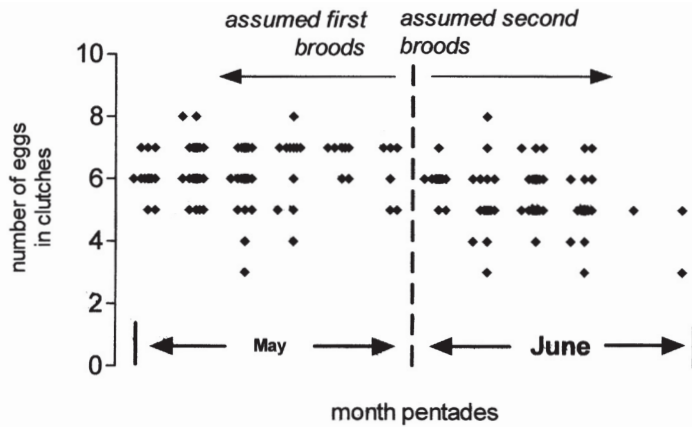


Fig. 3. Seasonal distribution of number of eggs in clutches in month pentades, ($n = 172$ nests).

fledged in more than 50% of nests (Table 3). The difference between ‘first’ and ‘second’ broods was not significant in any of the tested fledging variables.

Fledging success did not significantly differ from hatching success (total nest failure binary variables) either in ‘first’ broods (Fisher’s exact test, $P = 0.398$) or in ‘second’ broods ($P = 0.273$), or in all broods tested together ($P = 0.182$).

Table 3. Fledging success of common redstart broods calculated from the period between hatching and fledging: (a) total nest failure binary variable: no chicks fledged vs. one or more chicks fledged; (b) full/partial fledging binary variable: all chicks fledged vs. part of the brood failed to fledge; (c) mean fledging success and number of chicks failed to fledge per nest of the partially fledged nests. Data in the table are from a nest-box population from the northeast of Czech Republic, observed in years 1983–2002.

	All nests	‘First’ broods	‘Second’ broods	‘First’-‘Second’ broods comparison
(a)				
Number of observed nests	101	57	44	
Proportion of fledged nests	0.66	0.63	0.71	Fisher’s exact test $P = 0.526$
(b)				
Number of fledged nests	67	36	31	
Proportion of partially fledged nests	0.45	0.44	0.45	Fisher’s exact $P = 1.000$
(c)				
Fledging success of partially fledged nests (mean \pm sd)				
fledging success per nest	0.76 \pm 0.13	0.77 \pm 0.13	0.75 \pm 0.13	$t_{28} = 0.41$ $P = 0.690$
total number of chicks lost per nest	1.37 \pm 0.84	1.47 \pm 0.99	1.25 \pm 0.62	$t_{28} = 0.66$ $P = 0.516$

Overall nest success

The overall nest success (including the nests of unknown time of failure) was 45.1%. Some 41.1% of ‘first’ broods and 51.9% of ‘second’ broods survived to fledging. The mean number of chicks fledged per successful nest was 5.42 chicks (SD = 1.37, $n = 67$ nests) overall, with 5.94 chicks (SD = 1.41, $n = 36$ nests) in ‘first’ broods and 4.84 chicks (SD = 1.07, $n = 31$ nests) in ‘second’ broods. The difference between ‘first’ and ‘second’ broods was significant ($t = 3.54$, $df = 65$, $P = 0.001$).

Examining the effects of variables on overall nest success, only mean air temperature (28 days mean after clutch completion) in linear and squared terms was left in the final multiple logistic regression model. The date of first egg, precipitation, clutch size and year of observation had negligible effect and were eliminated from the model (Table 4). An optimum air temperature for a successful nest, calculated from a logit function of the final model, was 17.7°C. The values of temperature of the tested data set ranged from 11.3°C to 22.3°C (median = 15.9°C). All broods started and reared during periods of extreme temperatures were unsuccessful.

Table 4. Effects of first-egg-laying date, number of eggs in a clutch, precipitation, air temperature and year of observation (treated as continuous) on the binary nest success. Weather variables are sums/means of 28 day interval after clutch completion. Independent variables in the final model of multiple logistic regression were selected by backward elimination at the significance level of $P = 0.1$. Data in the table are from a common redstart nest-box population from the northeast of Czech Republic, observed between years 1983–2002, ($n = 90$ nests).

	Parameter estimate	SE	χ^2	P
Null model				
Intercept				NS
Egg-laying initiation + egg-laying initiation squared				NS
Clutch size + clutch size squared				NS
Precipitation + precipitation squared				NS
Air temperature				< 0.05
Air temperature squared				< 0.05
Year of observation				NS
Final model				
Intercept	-30.03	13.40	5.02	0.025
Air temperature	3.45	1.56	4.87	0.027
Air temperature squared	-0.10	0.05	4.67	0.031

Discussion

Egg-laying

The beginning of the redstart breeding season was highly synchronised, increasing rapidly from the last day of April to a peak in the second May pentade. A correlation between the start of breeding and air temperature has been documented previously but there are differences depending on biotope, latitude and area of distribution (Ruiter 1941, Balát 1976, Pulliainen et al. 1982, Järvinen 1983, Menzel 1984, Levin & Gubin 1985, Winkel 1986, Huhta & Jokimäki 2001). In our study, the earliest clutches in a season were started, on average, on 6 May at a temperature of 14.9°C. In Finland, the earliest clutches were started on 11–15 May at an average temperature of 9.5°C in the south

(60°–62°N) and on 26–30 May at 3.5°C in the north (69°N, 20°E) (Järvinen 1983). In summary, published studies indicate that egg-laying is initiated by an interaction of habitat and weather in spring, rather than by one factor alone.

The most striking difference between northern and southern redstart populations is the production of only one brood per season in northern populations (Fennoscandia) but frequently two broods per season in southern populations (central Europe) (e.g. Järvinen 1978, Pulliainen et al. 1982, Glutz von Blotzheim et al. 1988). Data on second broods are not plentiful and differ greatly among studies in southern redstart populations. One rare case of a second brood is known even from Finland (Sundelin cited in Pulliainen et al. 1982). The proportion of pairs which started second broods ranged from 9.4% to 50% in central Europe (Berndt & Frieling 1939, Balát 1976, Menzel 1984, Winkel 1986, Kurths cited in Glutz von Blotzheim et al. 1988) but it was only 4% in Holland (Ruiter 1941). The most obvious explanation of the difference, especially between northern and southern populations, is the time constraint dictated by the duration of the vegetation period. Eight of ten documented second broods in Holland (Ruiter 1941) occurred in one season with favourable weather conditions when breeding had started extremely early. However, it can be questioned whether the threshold difference in number of broods per season between populations in central Europe and southern Finland (60°–62°N) (Järvinen 1983) could be explained by just an additional week of potential breeding season in our population. The production of two broods per season, together with the laying of smaller clutches, could represent a different parental reproductive strategy in a conditions of short daylight period and under high nest predation (see below). The interpretation of the large variability in the proportion of second broods in studies from neighbouring areas in central Europe remains unclear and cannot be readily explained by different weather conditions in the years of study or by different methods of estimation. Data on adult survival rates in different populations is necessary for a more thorough knowledge on redstart reproductive strategies.

The mean time interval between laying of the first egg in first and second broods was very similar in all reported cases and ranged between 32.0 and 39.8 days (Ruiter 1941, Löhrl 1976, Menzel 1984, Winkel 1986). As the breeding season has two distinct peaks, with an interval which corresponds to the time gap between laying of first and second clutches, we believe our estimate of the proportion of second broods is realistic. Although replacement clutches were certainly a large proportion of all observed breeding attempts, we suppose they did not bias markedly the ratio of first to second clutches as the probability of nest failures was similar throughout the whole breeding season, i.e. they did not differ significantly between incubation and nestling periods and between the May and June broods. The estimated value of 65.4% of the pairs with second broods is by far the highest of all published studies.

Clutch size

The clutch size is reported to be higher in northern than in southern redstart populations (e.g. Järvinen 1978, Pulliainen et al. 1982, Menzel 1984), supporting Lack's theory that mean clutch size increases with latitude (Lack 1947). The mean clutch size in our study occurred within the known variability of the species and supports the north-south trend. The smallest average clutch size of 5.64 eggs was observed in populations in southeastern Czech Republic (49°N, 17°E) (Balát 1976, Pulliainen et al. 1982) and the largest of 6.89 eggs in northernmost part of Finland (69°N, 27°E) (Veistola et al. 1996). Large

broods in northern populations may be raised because continuous daylight allows the parents to collect food for longer (Lack 1947, Hannila & Järvinen 1987). According to Slagsvold (1982), differences in clutch size are rather due to selection caused by heavy predation. When the probability of total nest failure is high, parents may invest in smaller clutches and reserve more energy for possible replacement/second breeding attempts. This might be the case in populations of central Europe, where overall nest predation rates are very high (Balát 1976, present study). The number of eggs in second clutches is smaller than in the first clutches (Boubier 1925, Ruiter 1941, Menzel 1984, Winkel 1986) but the decrease in clutch size with season also occurs in single-brooded populations (Pulliainen et al. 1982, Järvinen 1983).

Hatching success

The hatching success in our restart population was amongst the lowest recorded in a range of studies. Although hatching success, including total nest failures, was greater in northern than in southern restart populations, the frequency of partial hatchings or the number of eggs lost per nest reached similar values across all studies (Balát 1976, Hudec 1983, Järvinen 1983, Menzel 1984, Winkel 1986, Pulliainen et al. 1994, Veistola et al. 1996). Especially in southern populations, egg losses were mostly due to total nest failure (i.e. mostly by nest or parent predation) rather than the destruction or failure of individual eggs in a brood.

Fledging success

Fledging success, including total nest failures, was greater in northern than in southern populations (Balát 1976, Järvinen 1983, Menzel 1984, Pulliainen et al. 1994, Veistola et al. 1996). Among successful broods, the proportion of only partially fledged broods in our study was very high (45%), even in comparison with other central European data (15–16.4%, Hudec 1983, Menzel 1984). The partial losses may be caused by parasite infections or sibling competition (Menzel 1984) rather than bad weather conditions as the chicks are able to survive even extremely cold seasons in subarctic areas (Pulliainen et al. 1994).

Although total hatching and fledging success varies among studies, fledging success is usually a bit higher than hatching success (Balát 1976, Järvinen 1983, Menzel 1984, Pulliainen et al. 1994) but there are also contrary results (Glutz et al. 1988). The reasons for failures at different stages of the breeding cycle are not well understood.

Overall nest success

In most studies, breeding success was calculated per egg and ranged between 46% and 89%. The values were lower in populations from central Europe, which do not overlap with those from populations in the north (Fennoscandia) (Medell 1961, Balát 1976, Järvinen 1983, Menzel 1984, Winkel 1986, Pulliainen et al. 1994, Veistola et al. 1996, Huhta & Jokimäki 2001). The large differences in breeding success between northern and southern populations are undoubtedly caused by difference in predation rate. The results of our study are at the lower end of the known range of breeding success. While the frequency of total nest failures was 11.8% (overall nest success = 88.2%) in the study of Järvinen (1983) (69°N, 20°E), in our study 54.9% of nests failed before fledging. Although

in the study of Veistola et al. (1996) the breeding success was affected by changing predation rate which depended on population cycles of small rodents in northern Finland, the proportion of predated nests was very low.

Nest success was significantly affected by mean air temperature during individual breeding cycles in the logistic regression model in our study. Nest success was highest at temperatures close to the mean value of the temperature range. As the breeding success of redstarts in both egg and nestling periods was not lower even in extremely cold subarctic conditions (Pulliainen et al. 1994), we suppose the effect of low temperature is indirect and rather indicates other environmental differences in breeding territory which were not recorded (e.g. number of predators, availability of food). We have no clear explanation for the negative effect of high temperatures detected in our study which has not been documented so far. Veistola et al. (1996) observed significant negative effects of rainfall on chick mortality. The effect of total precipitation on nest success in our study was not significant.

The number of chicks fledged per successful brood was higher in northern than in southern populations, which reflects higher numbers of eggs per brood in the north (Järvinen 1983, Menzel 1984). When total nest failures are included, the difference is much larger even when the chicks of first and second broods in southern populations are summed together. The average number of fledged chicks per season and breeding pair (seasonal breeding productivity) was 5.0–5.6 chicks in northern Finland (Järvinen 1983, Veistola et al. 1996) but only 3.0–4.9 chicks in central Europe (Balát 1976, Menzel 1984, present study). The production of two broods per season does not therefore compensate for the latitudinal differences in clutch size and breeding success.

Long-term changes

There were no changes in either the start of the breeding season or nest success over the 20 years of this study. Changes might be expected due to the rise in air temperature caused by global warming. For example, the onset of the breeding season, which is affected by air temperature, could become earlier spring over time, but this was not detected in our study. In other studies, differences in breeding parameters were documented between individual seasons but these were largely explained by specific weather or ecological conditions (Pulliainen et al. 1994, Veistola et al. 1996). There is no evidence that the parallel decrease in populations documented throughout the Europe (Berndt & Winkel 1979, Järvinen 1981, Winkel 1986, Hagemeyer & Blair 1997) is reflected by any changes in breeding biology of the species.

Acknowledgements

We are grateful to Marek Špinka, Karel Weidinger and two anonymous referees for their valuable comments on the manuscript.

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