

The influence of male age and phenology on reproductive success of the red-breasted flycatcher (*Ficedula parva* Bechst.)

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I studied arrival time, breeding phenology, and breeding success in relation to the age class (second year and older) of male red-breasted flycatchers for six breeding seasons (2000–2005) in the primaeval Białowieża Forest, eastern Poland. Older males, i.e. older than two years (ASY), arrived on average five days earlier than younger, second-year (SY) males. Moreover, early-arriving ASY males and experienced males were more likely to pair than were SY males and males that arrived later. Arrival time and age of males also influenced the first egg date of their mates. Arrival time, first egg date and age of male, however, did not influence clutch size, breeding success, or the number of offspring fledged. The richness and abundance of food under natural conditions may reduce the influence of age and experience on feeding effort and, as a consequence, reproductive success. High predation pressure may favour a “no restraint” breeding strategy and young birds should take full advantage of every breeding opportunity.

Introduction

In addition to environmental conditions, individual characteristics of birds like age, quality, and body condition can influence reproductive parameters. Age appears to be one of the most important factors; older individuals often establish territories earlier, mate more often (Harvey *et al.* 1979, Potti & Montalvo 1991) and raise more fledglings (Pianka & Parker 1975, Curio 1983, Seather 1990). Age-dependent reproduction may result from superior foraging abilities (Stutchbury & Robertson 1987, Burger 1988, Pyle *et al.* 1991, Desroshers 1992) or better predator avoidance behavior (Pyle *et al.* 1991) of older birds. This

phenomenon is explained by three hypotheses: (1) the disappearance of weak phenotypes, (2) increases in effort with age, and (3) constraints on younger individuals (Forslund & Pärt 1995).

Timing of breeding is another factor that influences reproductive success. In migratory bird species, breeding phenology is often influenced by arrival time. Arrival time can be influenced by environmental conditions such as temperature (Huin & Sparks 2000, Mitrus *et al.* 2005) or characteristics of individual birds (Møller 1994a, Stolt & Frasson 1995, Møller *et al.* 2003). Birds that arrive and breed earlier may obtain advantages such as higher quality partners or territories (Aebischer *et al.* 1996, Smith & Moore 2005),

and this can, in turn, increase clutch size and numbers of fledglings (Perrins 1970). Timing of arrival and breeding is often also related to the age and quality of the individual. Usually, older males arrive on breeding areas earlier (Lozano *et al.* 1996, Potti 1998, Mitrus 2004, Smith & Moore 2005) and older females initiate egg-laying earlier (Harvey *et al.* 1979, Perrins & McCleery 1985, Nol & Smith 1987).

The red-breasted flycatcher *Ficedula parva* is a migratory, cavity-nesting passerine that breeds in Europe and Asia (Cramp & Perrins 1993) and winters in the Indian sub-continent (Mitrus *et al.* 2005). Red-breasted flycatchers are not a well-studied species. Most studies have focused on basic biology and breeding ecology (Weber 1958, Aleknonis 1976, Byshnev & Stavrovsky 1998, Mitrus & Soćko 2004).

The aim of this study was to test the hypothesis that reproductive effort increases with age in male red-breasted flycatchers. To determine the influence of age in males, I compared arrival time, phenology, and breeding success under natural conditions in primaeval lowland temperate forest.

Methods

Observations were carried out from 2000 to 2005 in three study plots (total area 79.5 ha) located within Białowieża National Park (NE Poland, 52°41'N, 23°52'E). The study area is dominated by old-growth oak–lime–hornbeam *Tilio (Quercus)–Carpinetum* stands characterised mainly by hornbeam *Carpinus betulus*, Small-leaved lime *Tilia cordata*, pendunculate oak *Quercus robur*, Norway maple *Acer platanoides* and Norway spruce *Picea abies*. Many standing and fallen dead trees are present (Wesołowski *et al.* 2002).

Early in the breeding season, one to four persons searched for newly arriving males every day, in the same places, by listening to the songs of individual red-breasted flycatchers. I documented the arrival date as the day that a male was first recorded singing in a territory. Only those territories where males were sighted/heard on at least three consecutive days were considered occupied, and only these were included in the

analyses. In the statistical analyses, in each year, I used the arrival date of the first male to arrive as day 1. The following days of the breeding season were numbered sequentially from this day. Arrival and laying dates varied across years and thus were standardized as: observed value – yearly mean/yearly SD. Each male was aged by plumage characteristics. Older males (after-2nd-year, ASY) have orange patches on the breast while young males (2nd-year, SY) do not (Svensson 1992). Males were uniquely ringed using a combination of aluminum and colour-coded rings. Most males were captured after arrival, but before mating. Each year ~60% of males were individually marked and in the next year 20% to 25% of these males returned to the breeding area. Unmarked males were recognized by plumage and song characteristics. After arrival, territories were checked every day to determine mating success and to observe breeding behaviour. I located nests by following females during nest construction, searching territories, and following adults that were tending young. All pairs bred in natural nest-sites (Mitrus & Soćko 2004), there were no nests-boxes. I visited nest niches to determine clutch size, number of nestlings, and breeding success (success or failure). The first laid egg of each clutch was either directly detected or, if nests were discovered during the egg laying period, I calculated the first egg date using the assumption that one egg was laid per day (Cramp & Perrins 1993). If at least one nestling was observed just before the expected fledging date, the nest was considered to be successful. Breeding success was determined either by direct observation of fledged nestlings or by observations of nestlings in the nest just before fledging (on day 9 or 10 after hatching) from nests that lacked evidence of predation. Because of the danger of observers causing earlier fledging, the number of fledglings was determined as the number of nestlings observed on day 9 or 10 after hatching. Losses through predation were assessed from shells, dead nestlings with damaged bodies, lack of eggs or nestlings and ruffled or violated nest material, and lack of eggs or nestlings when they should have been in the nest.

Red-breasted flycatchers breed only once per season (Cramp & Perrins 1993). Replacement clutches were not included in the analysis. They

were recognized when new nest building was observed in the same territory after loss of the first brood.

I used Student's *t*-tests to assess variation in arrival time, laying date, clutch size and number of fledglings, and analysis of variance to assess variation in clutch size and number of fledglings in relation to year and age of male. I used logistic regressions for binary dependent variables (mating and breeding success in relation to arrival time or laying date). Data were tested for normality with the Shapiro-Wilk test. Chi-square test was used to compare pairing and nest success between groups of males. A significance level of $P = 0.05$ was chosen for all statistical tests. Statistical analyses were performed using Statistica for Windows version 5.0.

Results

Arrival time

The earliest arrival of a male occurred on 29 April 2000 and the latest arrival was observed on

7 May 2003 (Table 1). During six seasons, the arrival times of 64 SY and 208 ASY males were determined. Older (ASY) males arrived significantly earlier (on average, 5 days) than SY males (Table 2). In every year, SY males arrived later (on average, from 3 to 8 days; Fig. 1).

Mating success

Older (ASY) males were significantly more likely to pair than were SY males ($\chi^2 = 4.21$, $df = 1$, $P = 0.04$); 58% of ASY and 42% of SY males paired, respectively. The likelihood of a male obtaining a mate was significantly affected by the arrival time (logistic regression: $\chi^2 = 6.40$, $df = 1$, $P = 0.02$). Males that obtained mates arrived, on average, one day earlier than did males that did not pair (paired: mean = 8.3, $N = 116$, $SD = 4.83$ versus unmated: mean = 9.7, $N = 9.7$, $SD = 5.40$). In ASY males, mating success depended on the arrival time (logistic regression: $\chi^2 = 5.67$, $df = 1$, $P = 0.02$), but no such relationship was observed in SY males (logistic regression: $\chi^2 = 0.79$, $df = 1$, $P = 0.37$).

Table 1. Yearly variation in arrival times of older (ASY) and younger (SY) males.

Year	Old (ASY)				Young (SY)			
	<i>N</i>	Mean	Range	SD	<i>N</i>	Mean	Range	SD
2000	31	07.05	29.04–15.05	3.88	10	12.05	5.05–15.05	4.61
2001	46	06.05	30.04–21.05	5.26	14	09.05	03.05–21.05	5.08
2002	43	08.05	2.05–16.05	3.68	13	13.05	1.05–19.05	3.45
2003	29	11.05	07.05–19.05	3.27	6	15.05	13.05–17.05	1.90
2004	32	08.05	01.05–22.05	5.88	14	17.05	08.05–22.05	3.99
2005	27	14.05	01.05–21.05	4.59	11	17.05	11.05–21.05	3.32
Total	208	09.05	29.04–22.05	5.25	68	14.05	03.05–22.05	5.05

Table 2. Comparison of phenology, clutch size, and number of fledglings of older (ASY) younger (SY) male Red-breasted flycatchers. * $P < 0.001$.

	Old (ASY)				Young (SY)				<i>t</i> -test
	<i>N</i>	Mean	Range	SD	<i>N</i>	Mean	Range	SD	
Arrival time	208	-0.23	-3.20–2.44	0.94	64	0.76	-0.98–2.29	0.77	-7.63*
Laying date	46	-0.08	-2.22–2.10	1.02	20	0.22	-1.55–1.51	0.81	-1.20
Number of eggs	43	5.9	5–7	0.66	16	5.9	5–7	0.66	0.27
Number of fledglings	32	5.5	4–7	0.72	14	5.3	3–6	1.14	0.51

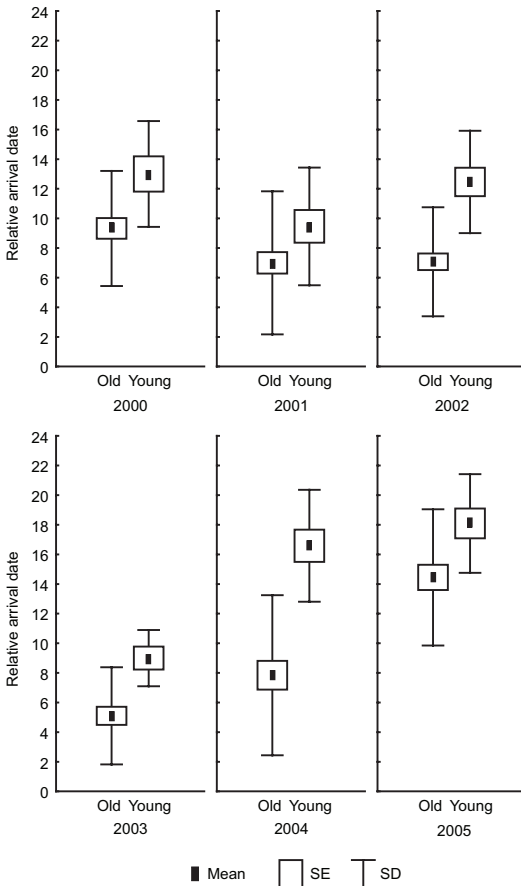


Fig. 1. Arrival dates of younger (SY) and older (ASY) male red-breasted flycatchers.

Timing of breeding

Usually red-breasted flycatcher females start to lay eggs in the second half of May. The earliest first egg was observed on 5 May 2001, and the latest on 12 June 2002 (Table 3). I determined first egg dates for 46 females that paired with ASY males and 20 females that paired with SY males. Females that paired with SY males initiated egg laying, on average, almost 3 days later, but this difference was not statistically significant ($t = 0.23$, $df = 64$, $P = 0.83$, Table 2). Females that mated with early-arriving males, irrespective of age of males, initiated egg laying significantly earlier ($r = 0.36$, $N = 54$, $P = 0.007$, Fig. 2). The same pattern was observed for the clutches of ASY males ($r = 0.32$, $N = 41$, $P = 0.04$), but no such relationship was found for SY males ($r = 0.19$, $N = 13$, $P = 0.57$).

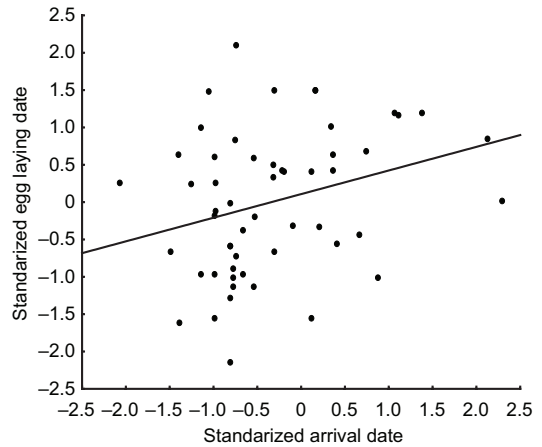


Fig. 2. Relationship between arrival date and first egg date of red-breasted flycatchers.

Clutch size

Clutch size ranged from 5 to 7 eggs and I found no difference in the number of eggs laid by females paired with ASY and SY males (Table 2). Clutch size was not influenced by year ($F_{5,52} = 0.97$, $P = 0.44$), male age ($F_{1,52} = 0.04$, $P = 0.84$), male arrival date ($r = -0.02$, $N = 47$, $P = 0.92$), or first egg date ($r = -0.02$, $N = 49$, $P = 0.91$).

Number of fledglings

I determined the number of nestlings that fledged for 32 clutches reared by ASY males and 14 clutches reared by SY males. On average, more nestlings of older males fledged, but this difference was not statistically significant (Table 2). The number of fledglings was not influenced by year of study ($F_{5,31} = 1.99$, $P = 0.21$), age of male ($F_{1,31} = 1.39$, $P = 0.21$), arrival time ($r = 0.19$,

Table 3. Yearly variation in laying dates of the red-breasted flycatcher.

Year	N	Mean	Range	SD
2000	4	18.05	13.05–27.05	6.30
2001	8	19.05	05.05–31.05	8.36
2002	21	27.05	14.05–12.06	9.65
2003	16	25.05	16.05–30.05	4.70
2004	14	27.05	20.05–03.06	4.97
2005	8	22.05	11.05–28.05	5.23

$N = 35$, $P = 0.27$), or timing of laying ($r = 0.03$, $N = 38$, $P = 0.85$).

Breeding success

I determined the success or failure (breeding success) of 87 nests of ASY and 27 nests of SY males. Sixty three percent of nests of young males and 48% nests of old males were successful, however, these differences were not significant ($\chi^2 = 1.78$, $P = 0.13$). Breeding success was related to arrival time (logistic regression $\chi^2 = 4.06$, $df = 1$, $P = 0.04$), but not to first egg date (logistic regression: $\chi^2 = 0.19$, $df = 1$, $P = 0.66$). Predation caused the majority of nest failures (82% of losses). All losses in SY males' nests were due to predators, but predation was only detected for 82% of ASY males' nest losses. The remaining 18% of ASY nests were apparently deserted.

Discussion

I found that older male red-breasted flycatchers arrived on breeding territories earlier than did younger males, and that both age and arrival time influenced pairing success. Further, male arrival date, but not male age, influenced the first egg date of females. Within mated pairs, however, variance in reproductive success was not influenced by male age or arrival date, and this may be due to high levels of predation in natural cavities of the primaeval forests of Białowieża National Park.

Date of arrival on the breeding grounds is one of the many factors that influence reproductive success in birds. Usually, early arriving individuals gain higher quality territories (Potti & Montalvo 1991, Aebischer *et al.* 1996, Smith & Moore 2005), are more likely to pair (Møller 1994b, Lozano *et al.* 1996, Kokko 1999), mate with females that breed earlier (Potti 1998) and produce more fledglings (Perrins 1970, Slagsvold & Lifjeld 1988). Patterns of arrival are often related to physical condition or age. Higher quality and older males usually arrive earlier (Møller 1994a, Stolt & Franson 1995, Mitrus 2004). My data is consistent with past research

on other passerine species and demonstrates that older male red-breasted flycatchers arrive earlier than younger males. In this species, however, early arrival time is not related to wing length or body condition of birds (C. Mitrus unpubl. data) or characteristics (tree species composition, density, thickness of living and dead trees) of the territories (Mitrus *et al.* 2006). But early arrival can give other advantages to males. Males that arrived early usually also mated earlier and their females initiated earlier egg laying. Owing to high predation pressure in the Białowieża Forest, nest losses are also high, but early breeders have more time and hence the chance to attempt repeat broods.

Arrival time, however, did influence male pairing success, suggesting that males that arrive earlier are able to better attract females. Many unpaired males suggested that in this area and in this population, males are more numerous than females and later arriving males probably have a lower chance of finding a mate. Older males might be more likely to find a mate because they have more ornamental plumage traits including an orange breast and blue plumage underneath the eyes. There is no evidence for carotenoids being the source of the orange patch in older males. However, the insect diet of red-breasted flycatchers suggests that melanin might be the origin of this ornament. In other species, ornamental plumage signals reliable information to females about male age, experience, and mate quality (Kokko 1998, Prolux *et al.* 2002, Sieferman *et al.* 2005). However, young males can have advantages from dull plumage coloration. Without the orange patch on the breast, they are indistinguishable from females. Such a pattern can reduce aggressive behaviour from older and stronger males (Hill 1989). Female mimicry and status signaling have been suggested as hypotheses to explain delayed plumage maturation (Rohwer *et al.* 1980) and have been supported by observation and experimental studies in some other species (Slagsvold & Saetre 1991).

Further, because ASY males have survived at least two years, they could be signaling genes for superior survivorship to females. Indeed, preferences for older males have been documented in many species (Manning 1985, Bradley *et al.* 1995), including the closely-related pied

flycatcher *Ficedula hypoleuca* (Berndt & Sterner 1971, Potti 2000). Older male red-breasted flycatchers are probably also more experienced than younger males and, like birds of other species, may be better foragers or provide for young more often (Clutton-Brock 1991, Pyle *et al.* 1991, Desrochers 1992, Pärt *et al.* 1992).

Timing of breeding may depend on many factors. At the population level, environmental conditions such as ambient temperature and food abundance influence timing of breeding (Wesołowski 1998, Meijer *et al.* 1999, Mitrus 2003). In this study, first egg dates differed between years suggesting that environmental characteristics influenced breeding phenology. In the Białowieża Forest, spring temperature can vary significantly from year to year and this fact affected the arrival time of male red-breasted flycatchers (Mitrus *et al.* 2005) and the laying date in a closely related species, collared flycatcher *Ficedula albicollis* (Mitrus 2003). At the individual level, characteristics of birds can influence first egg date. Female red-breasted flycatchers initiate egg laying earlier when mated with males that arrived on the breeding grounds earlier. Although the age of the female red-breasted flycatchers was not known, this factor may also influence first egg date (Verhulst *et al.* 1995, Blums *et al.* 1997, Mitrus 2005). Older females are usually more experienced and can prepare and collect resources for egg production more quickly. Although many studies report that females that pair with older males commence breeding earlier (Harvey *et al.* 1979, Perrins & McCleery 1985), I found no effect of male age on timing of breeding in female red-breasted flycatchers.

Clutch size was not influenced by year, male age, or timing of egg laying in red-breasted flycatchers, suggesting that this trait is not influenced by changing environmental conditions. Moreover, within pairs that successfully fledged at least one offspring, I found no influence of year, male age, or timing of egg laying on the number of offspring fledged. Breeding success in natural stands of the Białowieża Forest is highly influenced by predation (Tomiałojć 1991, Wesołowski & Tomiałojć 2005) and, by far, predation was the most common cause of nest failure in red-breasted flycatchers. Predation is the main factor affecting breeding success also

in other species breeding in this forest. In secondary cavity-nesting birds, total nest losses due to predation ranged from 71% in marsh tit *Parus palustris* to 91% in collared flycatcher (Wesołowski & Tomiałojć 2005). The Białowieża National Park is characterized by the presence of almost the entire list (without brown bear *Ursus arctos*) of European forest predators which predate birds' nests (Tomiałojć & Wesołowski 1990, Jędrzejewska & Jędrzejewski 1999). Rodents, mustelids and birds, especially woodpeckers *Dendrocopos* sp. and jay *Garullus glandarius*, are the most common predators of cavity-nesting birds (Walankiewicz 2002, Wesołowski 2002, Wesołowski & Rowiński 2004). It is possible that differences in reproductive success due to age and arrival date are masked by the high predation rates in the natural stands and natural nesting cavities of the red-breasted flycatchers of the Białowieża National Park. A lack of differences between young and old males in breeding effort and success was observed also in collared flycatcher populations breeding in the Białowieża Forest (Mitrus 2004).

High predation pressure may favour a "no restraint" breeding strategy. The red-breasted flycatcher is a small, short lived species; young birds should take full advantage of every breeding opportunity because their lives are short with uncertain future reproductive potential. Furthermore, richness and abundance of food (Rowiński & Wesołowski 1999) may reduce the influence of experience on feeding effort and, in consequence, on reproductive success in this species.

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