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No effect of age of males on reproductive success of the collared flycatcher *Ficedula albicollis*

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A b s t r a c t . During five years (1992–1996) the effect of age of collared flycatcher males on arrival time, quality of nest site, partial losses, feeding effort and reproduction were examined in the primaeval, mature (170–250 year old) oak-lime-hornbeam forest of Białowieża National Park. The males were divided into two age groups: males with brown primaries and wing covers were aged as young, and males whose wings were uniformly black were aged as old ones. Only the arrival date and the clutch size were significantly different between the groups of males but other breeding features were very similar. These results may be explained by a short life-span of flycatchers and by conditions in the Białowieża National Park. A surplus of good natural cavities reduced competition between young and old males, and a surplus of food could reduce differences in foraging abilities. A high predation rate was the main cause of nesting losses. In such conditions, the strategy to take each opportunity of reproduction may lead to high life time reproduction success and can reduce potential differences in breeding success young and old males

Key words: collared flycatcher, age of male, breeding effort, predation, Białowieża Forest

Introduction

It is well known that reproductive success in animals improves with age (C l u t t o n - B r o c k 1988, S e a t h e r 1990, M a r t i n 1995). Intensive studies of the influence of age or experience on reproduction have been conducted on birds. Numerous papers refer to long-lived species (e.g. N e w t o n et al. 1981, T h o m a s & C o u l s o n 1988, F o r e s t & G a s t o n 1996). Most reported that individuals improve results of reproductive success with age. Older males often mated earlier than younger ones because of earlier arrival on the breeding area (H i l l 1989, T h o m p s o n & H a l e 1991, L o z a n o et al. 1996), better territories (A l a t a l o et al. 1984, P o t t i & M o n t a l v o 1991, L u n d b e r g & A l a t a l o 1992) and more complicated song (L a m b r e c h t s & D h o n d t 1986). More experienced birds also raise more fledglings because they are more skilled in finding food (S t u t c h b u r y & R o b e r t s o n 1987, B u r g e r 1988, P y l e et al. 1991) and in avoiding predators (P y l e et al. 1991). Also, in cavity-nesting species, young individuals suffer from lower breeding success than older ones. Older females of the pied flycatcher *Ficedula hypoleuca* (L u n d b e r g & A l a t a l o 1992), the great tit *Parus major* and many other cavity-nesting birds (H a r v e y et al. 1979, M c C l e e r y & P e r r i n s 1988, E n o k s o n 1993) start breeding earlier, lay more eggs and also raise more fledglings. Similar results have been obtained in comparison between young and old males. Older individuals established territories earlier, mated more often and raised more nestlings than younger ones (H a r v e y et al. 1979, P o t t i & M o n t a l v o 1991, L u n d b e r g & A l a t a l o 1992).

This study is based on observations of the collared flycatcher *Ficedula albicollis*, a small passerine bird breeding in cavities of old trees or in nest-boxes. The breeding range of this species extends mainly in Central and Eastern Europe (Cramp 1993). A sharp dimorphism enables recognition of sex in the field. Furthermore, differences in plumage allow recognition one-year old and older males.

So far, studies on this species have been concerned mainly with basic biology and breeding ecology (i.e. Löhrl 1976, Gustafsson 1985, Walankiewicz 1991, Sachslehner 1995). Other studies related to the present paper concentrate mainly on the influence of age or of quality of female on reproductive success. However, papers referring to collared flycatcher males described problems connected with mating system, reproduction costs (Gustafsson 1989, Gustafsson et al. 1995, Pärt & Qvarnstrom 1997) and philopatry (Pärt & Gustafsson 1989, Pärt 1995).

The main aim of this study was to determine the influence of age of male collared flycatchers on their reproductive success.

Study Area

The data were collected in Bialowieża National Park ($52^0$41'N, $23^0$52'E), in a strictly protected area, that has never been cut and now is. Human activity is restricted only to a few tourist paths and to scientific studies. The study area (61.5 ha) was divided into two parts. In one (25.5ha) 60 nest-boxes were placed. In the other (36 ha) all cavity-nesters occupy only natural holes. The study area was dominated by old growth oak-lime-hornbeam characterised by 170–250-year-old stands (Tomiałojć 1991). Plots were bordered on one side by the edge of forest. The collared flycatcher is the most numerous breeding cavity-nester in oak-hornbeam forest (Walankiewicz et al. 1997, Wesołowski et al. 2003). The Białowieża Forest has several predators which take birds i.e. pine marten *Martes martes*, weasel *Mustela nivalis*, red squirrel *Sciurus vulgaris*.

Methods

Observations were conducted from 1992 to 1996. For determination of date of arrival, characteristic of cavities and predation rate only data from natural holes were used. Because of a lack of differences between nest-boxes and cavities in the breeding the biology of collared flycatcher (Mitrus 2003) data from both types of nests site were used for assessment of clutch size, number of fledglings, food provisioning and partial losses.

During the arrival period (from mid of April to about 20 May), every morning 2–4 persons looked for singing collared flycatcher males. Arrival data in 1992 were excluded because of the late start of observations in this year, after the first males had appeared. The day of arrival was assumed to be the day of the first observation of male singing and entering a cavity. In statistical analysis relative days were used. Each year the day when the first male arrived at the study plot was treated as day 1. On the basis of plumage characteristics, either males were aged as young (with brown primaries – one-year old) or old (with black primaries – two-year old and older; Svensson 1992).

Each tree with cavities where males were singing and entering was marked and its position was plotted on the map of the study plot. The cavities were visited later to describe their dimensions (height from the ground, entrance size, depth, bottom area) and to

determine the clutch size, partial losses and breeding success. The dimensions of the cavities were inspected and measured using a small mirror with lamp attached to bendable wire (W a l a n k i e w i c z 1991). The number of fledglings were obtained only for successful nests. Breeding success was determined on the basis of direct observation of fledged nestlings, observation of nestlings in the cavity just before fledging and from lack of traces of predation in the nest. If at least one nestling was observed before the expected fledging date, the nest was considered to be successful.

Losses through predation were assessed by observation of shells or perforated eggs, dead nestlings with damaged bodies, lack of eggs or nestlings and removed nest material or violated nest material, lack of eggs or nestlings in the period when they have been in the nest.

The role of a male in raising nestlings was determined by the rate and the share of male in feeding nestlings. Food provisioning was observed by binoculars over 30 min in the morning (6.00–9.00) under good weather conditions from distance of about 20 m. Observations were conducted three times for brood, when nestlings were 3–4 days old, 6–8 days old, and 12–14 days old.

Significance of differences was tested using Mann-Whitney U-test and analysis of variance (ANOVA).

Results

T i m e o f s e t t l e m e n t

The first singing males in Białowieża Forest are observed usually in the second half of April. The earliest arrival dates were recorded in 1994 and in 1995 (19 April), and latest (26 April) in 1996. During the study period the arrival time of 112 one-year old and 166 older males was determined.

Independently of the study year (pooled data) young males settled territories on average 4 days later than older ones ($z = -5.94$, $p < 0.001$). Half of them arrived up to 11 days after the first male, while half of older males arrived up to 6 days later. Except for one year (1993) one-year old males settled significantly later than older ones (Table 1).

Table 1. Relative arrival time of young and old males.

	Young			Old			
Year	N	Mean	SD	N	Mean	SD	U-test
1993	36	10.7	4.9	37	9.0	5.7	-1.74, ns
1994	27	10.8	5.1	46	7.3	5.9	-2.96 *
1995	28	12.9	6.4	42	6.8	5.7	-3.68 *
1996	21	11.8	4.5	41	7.8	4.4	-3.10 *
Total	112	11.3	5.1	166	7.6	5.3	

* – $p < 0.01$, ns – not significant

N e s t s i t e c h a r a c t e r i s t i c

Collared flycatcher males chose as a nest sites cavities in five species of trees: hornbeam, elm, lime, oak and spruce. No differences were found between young and old males in the

occupied tree species ($\chi^2 = 2.01$, $df = 4$, $p = 0.73$). Both young and old males most often (over 80%) chose cavities in hornbeam. No differences were found in cavity dimensions (height from the ground, diameter of entrance, depth, bottom area) occupied by young and old males (Table 2).

Table 2. Comparison of cavity dimensions of young and old males.

	Young			Old			
Cavity dimensions	N	Mean	SD	N	Mean	SD	U-test
Height above ground (m)	144	8.0	3.70	263	8.4	3.65	-0.81, ns
Entrance diameter (cm)	121	4.6	2.05	215	4.8	2.60	-0.84, ns
Cavity depth (cm)	117	20.9	10.98	215	22.0	10.56	-1.03, ns
Bottom area (cm^2)	119	97.9	71.62	208	97.6	74.00	-0.45, ns

Clutch size

The number of eggs varied from 4 to 8 in clutches of young males and from 4 to 9 in clutches of old males. Females mated with young males laid on average fewer eggs than females with older males (Table 3). The clutch size depended on the year ($F_{4,219} = 3.06$, $p = 0.02$) and on the age of males ($F_{1,219} = 4.69$, $p = 0.03$, Table 3). In all breeding seasons clutches of young males were smaller on average but differences were not significant. The date of settlement did not influence the number of eggs in clutches of young males ($r = -0.14$, $p = 0.36$, $N = 47$) or in clutches of old males ($r = -0.18$, $p = 0.13$, $N = 70$).

Table 3. Comparison of clutch size and number of fledglings of young and old males.

		Young			Old			
Year		N	Mean	SD	N	Mean	SD	U-test
1992	eggs	8	6.4	0.74	12	6.6	1.08	-0.11, ns
	fledglings	8	6.2	0.71	9	5.9	1.08	-0.48, ns
1993	eggs	25	6.2	1.00	27	6.6	0.63	-1.37, ns
	fledglings	22	5.1	1.17	20	5.9	1.42	-2.03*
1994	eggs	11	6.2	0.58	32	6.6	0.61	-1.7, ns
	fledglings	10	5.5	0.97	26	6.0	1.22	-1.13, ns
1995	eggs	20	6.5	0.69	44	6.5	0.70	-0.29, ns
	fledglings	20	5.3	1.80	42	5.5	1.31	-0.35, ns
1996	eggs	11	5.8	0.75	38	6.1	0.77	-1.01, ns
	fledglings	8	5.1	1.13	32	5.7	0.79	-1.06, ns
Total	eggs	75	6.2	1.33	129	6.4	0.75	
	fledglings	68	5.3	1.33	129	5.7	1.15	

* - $p < 0.05$, ns - not significant

Partial losses

Partial losses were recorded in 50.0% (out of 59) of nests of young males and in 49,2% (out of 124) nests old males. Partial losses of eggs in young male clutches varied from zero

to 16.7%, and in older males from 6.3% to 10.0%. Losses of nestlings varied from zero to 10.6% in both young and old males clutches. The age of male did not influence the partial losses ($F_{1,182}$ = 0.39, p = 0.53), but they were significantly affected by year of breading ($F_{4,182}$ = 2.27, p = 0,03). Losses during incubation as well as losses of nestlings did not depend on the age of male (respectively $F_{1,173}$ = 2.32, p = 0.13, $F_{1,154}$ = 0.06, p = 0.81) nor on the year ($F_{4,173}$ = 1.3, p = 0.27, $F_{4,154}$ = 1.7, p = 0.15).

The rate and the share of males in feeding nestlings

On average, males fed nestlings from 5 to 8 times per 30min. The rate of feeding depended on age of nestlings ($F_{2,146}$ = 16.4 p < 0.001) but not on the age of males ($F_{1,82}$ = 0.46, p = 0.5). Males fed most intensively nestlings in the age range of 6–9 days and before fledging (Fig. 1). Similarly to the rate, the share of feeding depended on the stage of development of nestlings ($F_{2,158}$ = 10.15, p < 0.001), but no influence of the age of male was observed ($F_{1,79}$ = 0.2, p = 0.65).

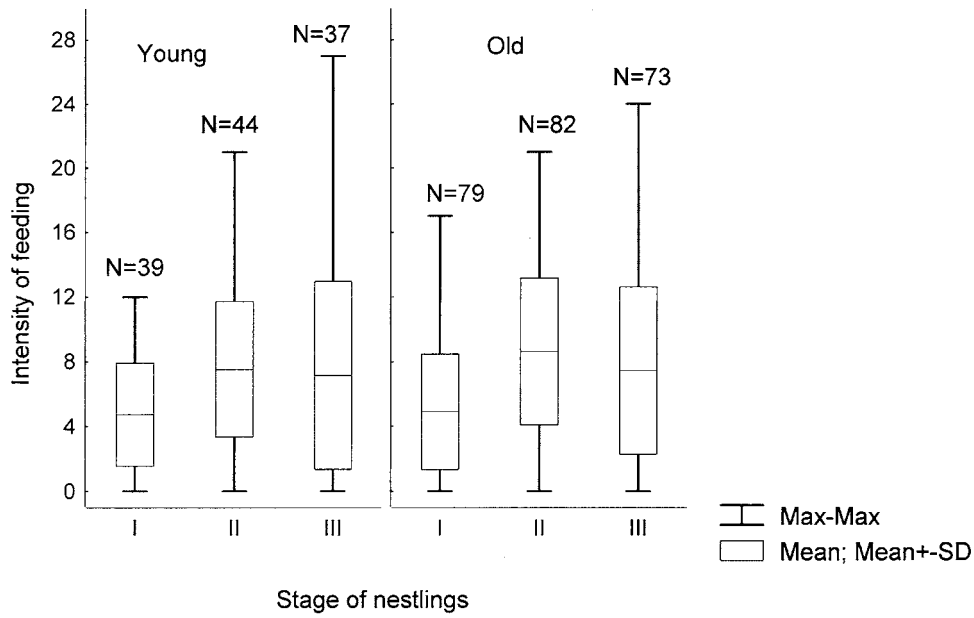

Fig. 1. Feeding effort of young and old male collared flycatchers in various ages of nestlings (I – nestlings 3–4 days old, II – 6–8 days old, and III – 12–14 days old).

Nest success

The proportion of successful clutches of young males ranged from 48.6% in 1993 up to 94,7% in 1992, and breeding success of old males in the same years was from 41.9 to 80.0%. However, the proportion of successful nests did not differ between old and young males. In general, 60.7% nests of young males and 53.6% nests of old males were successful. Predation was the main cause of losses (81.2%).

Number of fledglings

Productivity was determined for 197 nests (68 nests of young and 129 of old males). The number of fledglings depended neither on year ($F_{4,189} = 1.59$, $p = 0.22$) nor on the age of male ($F_{1,189} = 1.67$, $p = 0.2$). In some years (except 1992) productivity in nests of old males was on average higher, but differences were not significant, except for 1993 (Table 3). The number of fledglings in clutches of old males with 6 and 7 eggs was slightly higher than in young males' nests with the same number of eggs (Fig. 2) but differences were not significant (U-test, $z = -0.18$, $p = 0.85$; $z = -0.78$, $p = 0.43$).

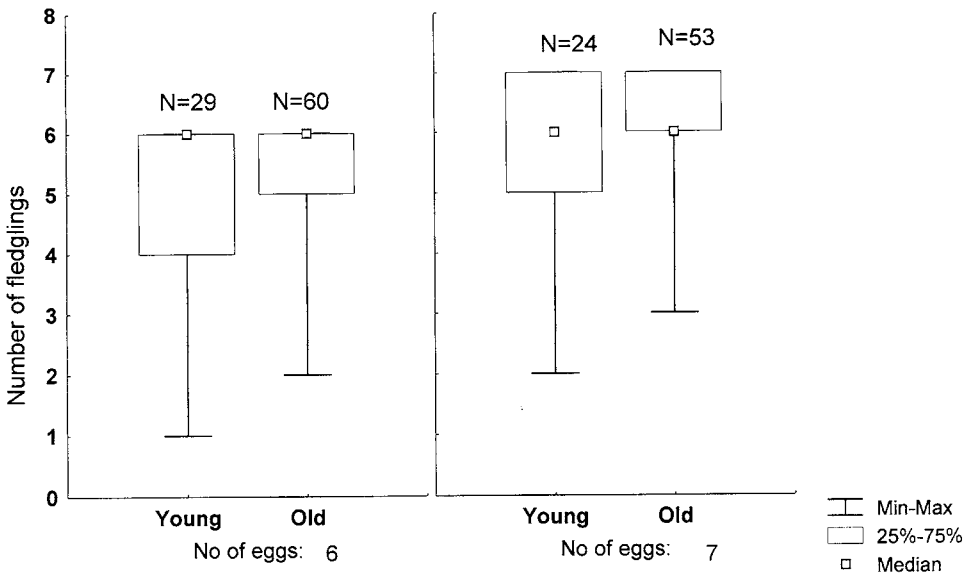

Fig. 2. The number of fledglings in clutches with 6 and 7 eggs for young and old male collared flycatchers.

Discussion

The pattern of earlier arrival of old males agrees with that observed in other European populations of the collared flycatcher (Löhrl 1976, Pärt 1995) and pied flycatchers (Lundberg & Alatalo 1992) as well as with other passerine species (Hill 1989, Thompson & Hale 1991, Lozano et al. 1996).

Hill (1989), studying black-headed grosbeak *Pheuctinus melanocephalus*, suggested that young males arrived later to avoid conflicts with old males. The collared flycatcher males are most aggressive during courtship, just before mating (Král & Bičík 1989). Young males arrived at a time when most old males were already mated. But small territories and plenty of available cavities allow young males to avoid aggression with other males. Delayed settlement may also be connected with a lack of experience of one-year old males. Males which bred in previous seasons visited first their known breeding place (Pärt & Gustaffson 1989), while young males without experience may have to spend more time searching for suitable nest sites. However, in Białowieża Forest with a surplus of cavities, young males need search for suitable nest site no longer than older males.

Earlier arrival may give some advantages, for example obtaining a good territory. In many species it has been observed that later arriving young males settled in marginal habitats (Potti & Montalvo 1991, Lundberg & Alatalo 1992, Johnson 1997). But in this study, the cavities of young males did not differ from cavities occupied by old males. It suggests little or no competition for the nest site, the result of abundance of old trees with plenty of cavities in the Białowieża Forest (Walankiewicz 1991, Mitrus et al. 1996).

In the Białowieża Forest, clutches of old males were on average larger than of young ones. Similarly, old males of great tit (Harvey et al. 1979), marsh tit *Parus palustris* (Smith 1993, Wesołowski 1998), pied flycatcher (Harvey et al. 1985) and of other species (Labedz 1984, Korpimäki 1988) have larger clutches than young males. The main reason for these patterns is probably the timing of laying eggs. Earlier arrival, earlier mating of old males and earlier start of egg lying by females mated with them may determine the greater clutch size (Harvey et al. 1979, McCleery & Perrins 1988, Enokson 1993).

The lack of differences in partial losses of eggs between clutches of young and of old males indicated a similar quality of individuals. But significant differences between years suggested the influence of weather factors such as ambient temperature and rainfall. In the collared flycatcher only females incubate egg. The level of partial losses during incubation may reflect mainly the differences in female quality. However at this time the male feeds the female and his attention may influence her condition, and indirectly on losses of eggs (Nilsson & Smith 1988, Potti & Merino 1996). Partial losses of nestlings may depend on weather conditions (Järvinen 1993, Siikamäki 1995), abundance of food as well as on the quality of parents. In the collared flycatcher it maybe influenced by the quality of both female and male because both participate in feeding nestlings. Losses of nestlings in Białowieża Forest did not differ between clutches of young and old males. This fact is supported by a similar feeding intensity in both groups of males.

No differences in the share and the rate of feeding were found between old and young males, as indirectly shows by a similar level of partial losses in clutches of both categories of males. In the pied flycatcher (Lundberg & Alatalo 1992) and in the male american redstart *Stegofaga rusticola* (Omland & Sherry 1994) a similar pattern was observed. But in other observations on collared flycatcher (Pärt et al.1992) and in other species, a lower participation of young individuals in feeding, and their reduced skill in food collecting were stated.

The number of fledglings was slightly lower on average in nests of young males than of old males. This fact is a consequence of differences in clutch size and of similar partial losses. But similar number of fledglings were observed in nests with the same clutch size. Breeding success under Białowieża Forest conditions depended mainly on the level of predation. However, the size of entrance and height above ground determine the safety of a nest (Nilsson 1984, Walankiewicz 1991, Wesołowski 1996). Young and old males occupied cavities similar in parameters. This fact influenced the lack of differences in the level of losses caused by predators. This result does not support observations of Pyle et al. (1991), who stated the improvement of skill of locating safe nest sites with age.

In this study, no differences in skills between old and young males were observed. Young males are as good as the old ones in choosing nest sites, feeding nestlings and

avoiding predation. The arrival time was the only variable significantly different between young and old males. This fact was probably the main reason for fewer eggs and fledglings in nest of young males. This phenomenon may be explained both by restraint and constraint hypothesis (C u r i o 1983). Later arrival or settlement may be the effect of constraint by shorter wings or by lack of knowledge on proper nest sites, but this fact may be an effect of avoiding competition or of restraint of reproduction effort, or both. Many papers reported lower energy expenditure and higher survival rates in birds reproducing fewer fledglings (C u r i o 1983, G u s t a f s s o n et al. 1995). In this study no evidence was found for restraint of effort by young males. Although there is no data on survival rate of male collared flycatchers breeding in Białowieża Forest, high predation pressure there should force males to take every chance for reproduction.

Similar reproductive success of young and old males may be partially the effect of lack of experience in some old males, because they did not mate in the first attempt of breeding. In a similar way this may influence quality of individuals. If we assume that best quality birds bred in the first year, than the reproductive success of groups of older individuals was influenced by poorer birds. But factors which may significantly equalize chances and improve effectiveness of young males were environmental conditions in natural stands of the Białowieża National Park: abundance of nest sites and food (outbreak of the Geometridae) and high levels of predation. Abundance of nest sites allowed young males to settle in good cavities and to avoid aggression from old males.

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