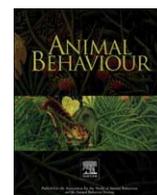


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Effects of extrapair paternity and sex on nestling growth and condition in the collared flycatcher, *Ficedula albicollis*

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Extrapair fertilizations (EPFs) have been found in most socially monogamous passerine species. EPFs are generally beneficial for males because they increase the number of sired offspring. The benefit accrued by females, however, is less obvious. Maternal benefits may involve fertility insurance, increased genetic variability of the offspring, and improved offspring quality via compatible genes or 'good genes'. In a Hungarian population of the collared flycatcher, we investigated whether the occurrence of extrapair young (EPY) in a brood could be predicted by the traits of the females or their social mates, and whether EPY were superior to their half sibs in terms of growth and fledging condition. We found that 55.7% of the broods contained EPY. The females' participation in extrapair copulations (EPCs) was not related to any of the characteristics of their mates (body size, condition, wing and forehead patch size). The EPY did not differ from their half sibs in any measures of offspring quality. The half sibs had similar embryonic and postembryonic growth and fledged with similar body condition. Female body size was related to extrapair paternity: larger females were less likely to produce mixed-paternity broods. This suggests that the role of female traits in EPCs deserves more attention. We also found that male nestlings grew faster than females, although females could catch up by the time of fledging, so we argue that sex-dependent development should be taken into account in studies using nestling growth as a measure of nestling quality.

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Although 93% of passerine species have a monogamous social mating system (Lack 1968), extrapair fertilizations (EPFs) have been found in the majority (86%) of these species (Griffith et al. 2002). While in some cases, males can lose paternity in their brood independent of their extrapair success (Delhey et al. 2003), within- and extrapair success are often positively correlated suggesting that extrapair copulations (EPCs) can increase the number of offspring that males sire (Gibbs et al. 1990; Kempenaers et al. 1997; Strohbach et al. 1998). However, the number of eggs a female can produce is strongly limited. Females have to invest a substantial amount of resources in the ova (Ojanen 1983), and costly incubation (Reid et al. 2000) is also exclusively their task in many species. The need for incubation may even set a physical limit to clutch size (Moreno et al. 1991; Engstrand & Bryant 2002). Furthermore, the hatchlings' need for parental care further limits brood size (Nur 1984). Thus EPFs are not expected to increase considerably the number of eggs a female produces. However, observations of

females seeking extrapair copulations (Wagner 1992; Gray 1996) suggest that they may still benefit from mating with nonpair males. Such benefits can be direct (e.g. parental investment in the offspring by the extrapair mate) or indirect (reviewed in Griffith et al. 2002). Indirect benefits may involve fertility insurance (Sheldon 1994; Gray 1997) and various types of genetic benefits. Females may, for example, participate in EPCs to increase the genetic variability of their offspring as a risk-spreading strategy (Williams 1975; Westneat et al. 1990), or they may seek extrapair fathers with compatible genes (Johnsen et al. 2000; Foerster et al. 2003). However, the most thoroughly studied hypothesis is that females try to gain 'good genes' for their offspring, which could then improve the survival (Hasselquist et al. 1996; Kempenaers et al. 1997) and/or future reproductive performance of the young (Schmoll et al. 2005). This, of course, requires that females are able to recognize males carrying these genes using phenotypic cues, for example secondary sexual characters (Møller & Ninni 1998).

One example of sexual character-dependent EPFs was found in the Swedish population of collared flycatchers. The male forehead patch size (a heritable and condition-dependent secondary sexual character; Gustafsson et al. 1995; Qvarnström 1999) predicted paternity in the broods (Sheldon et al. 1997a). Extrapair young sired by males with large patches fledged in better condition than their half sibs and the difference between the chicks increased with the

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difference in the forehead patch size between the social and extrapair fathers. In a Hungarian population of the collared flycatcher, one study showed that mates of males with small patches were more likely to participate in EPCs (Michl et al. 2002) just as in the Swedish study, but another study found no such relationship (Garamszegi et al. 2004a). The forehead patch size may be related to male quality in the Hungarian population as well (Garamszegi et al. 2004a); however, it is not positively correlated with body condition (Hegyi et al. 2002, 2006). In addition, the effect of wing patch size (a heritable, condition-dependent trait; Hegyi et al. 2002) on EPF patterns has not yet been tested in the Hungarian population. Therefore it is not clear how females benefit from EPFs. To investigate this, we examined the posthatching performance of extrapair and within-pair offspring in the Hungarian population of collared flycatchers. To our knowledge we are the first to examine the speed of embryonic growth in relation to paternity as well. In both cases, we controlled for the possible confounding effect of offspring sex, because females may adjust their brood sex ratio in relation to the same signals of attractiveness as they use in extrapair mate choice (Ellegren et al. 1996; but see Rosivall et al. 2004), and the sexes may differ in their growth rate even in monomorphic species (Martins 2004). In addition, the effect of sex on offspring performance is interesting per se, because it may explain the previously found seasonal shift in brood sex ratios in this population (Rosivall et al. 2004).

METHODS

Study Site and Species

Field data were collected in 2002 and 2003 from a nestbox-breeding population of collared flycatchers in the Pilis Mountains (47°43'N, 19°01'E), Hungary. The study plot is part of a continuous, unmanaged, oak-dominated woodland, a protected area of Duna-Poly National Park. The collared flycatcher is a small, hole-nesting, long-distance-migratory passerine bird that starts to breed in mid-April. Females usually lay five to seven eggs which hatch approximately 12 days after the last egg was laid. Nestlings usually fledge 14–15 days after hatching.

The collared flycatcher has a predominantly monogamous social mating system and in our study area fewer than 10% of the males are socially polygynous (Garamszegi et al. 2004b). However, the rate of extrapair fertilizations can be as high as 40% in our population (Michl et al. 2002).

Field Methods

We studied 45 broods (22 in 2002 and 23 in 2003). All eggs were numbered with a nontoxic permanent marker on the day of laying. All clutches were placed in an incubator (PL Machine SK75) 1 day before the expected hatching date and replaced with dummy eggs. Females accepted these dummy eggs as their own and continued the incubation. The original eggs were hatched in separated compartments at 37.2 °C and 70–80% humidity. All embryos that were still alive when placed into the incubator hatched successfully. We checked hatching every hour from 0415 to 2100 hours. For eggs hatching during the night we assumed that they hatched halfway between the last and the first checking. Each hatchling was marked individually on its breast with a permanent nontoxic pen and returned to its nest immediately, or early the following morning if it hatched during the night. Colour marking was randomized in relation to hatching order. We followed body mass increase of the nestlings in all broods from the day when the first chick(s) in a brood hatched (day 0) and the growth of the wing feathers in 34 broods from day 8 until fledging. Body mass (± 0.1 g) and the length of the third outer primary (± 0.5 mm) were measured every second

day. On day 14, body mass was measured in all broods, whereas the length of the third outer primary and tarsus length were measured in all but two broods.

Parents were captured using spring traps when their young were 10–12 days old. The tarsus length and body mass of both parents were measured. We also measured the size of the white plumage ornaments of males with a calliper. Forehead patch size was estimated as the product of height and width (Hegyi et al. 2002), while wing patch size was estimated as the sum of the visible lengths of white on the outer vanes of primaries 4–8 on the right wing (Török et al. 2003).

Sex Determination and Paternity Analysis

Blood samples (approximately 15 μ l) were collected from the brachial vein of 10–12-day-old nestlings. Parents were sampled on the same day as their young. For molecular sexing we used the primers 2550F and 2718R (Fridolfsson & Ellegren 1999) according to the protocol published in Rosivall et al. (2004). All of the adult samples were used as controls during molecular sexing and were always correctly sexed.

We assessed paternity by using four polymorphic microsatellite loci (Table 1). We modified the original thermal profiles slightly to improve PCR amplification (the modified protocols are available from B.R. on request). The PCR products were run on 6% polyacrylamide gels and visualized using a FluorImager (Molecular Dynamics Inc., Sunnyvale, CA, U.S.A.). The samples of all members of a family were run on the same gel so any mismatch in the genotypes between offspring and putative parents could be detected. Assuming Mendelian inheritance, we classified offspring as extrapair young if their genotypes did not match their putative father at one or more loci. Mutations are very unlikely to confound our results, because no single-locus mismatch was found between mothers and offspring, which could have been indicative of a high mutation rate.

Analyses of Nestling Performance Data

We obtained growth performance, sex and paternity data for 32 broods (13 and 19 broods in 2002 and 2003, respectively). Four of the parents were captured in both years, and to avoid pseudoreplication we included only one of their broods. In one brood, all the chicks were sired by extrapair males (at least two different individuals). Since in this case we cannot exclude the possibility that another male than the social mate was captured and sampled in the nestbox, this brood was omitted from all analyses.

Throughout the study, we used individual-based analyses (general linear mixed models) with brood identity as a random factor. When we analysed the effect of extrapair paternity on offspring growth and fledging size, only nestlings from mixed-paternity broods were included ($N = 87$ chicks). The effect of sex, however, was also analysed on a larger data set including 170 chicks. Because the effect of possible confounding factors on nestling performance, such as laying order, brood size and year,

Table 1

Polymorphism data at four microsatellite loci in the Hungarian population of the collared flycatcher

Locus	Number of alleles	Exclusion probability	Primer source
FhU2	17	0.755	Ellegren (1992)
FhU3	10	0.385	Primmer et al. (1996)
FhU4	18	0.692	Primmer et al. (1996)
PdO μ 5	13	0.745	Griffith et al. (1999)
Combined		0.988	

Exclusion probabilities were calculated by CERVUS 3.0 (Kalinowski et al. 2007).

were analysed in a previous paper using a larger data set (Rosivall et al. 2005), we included only those factors in the present analyses that were significant in the earlier study. Laying order had a significant effect on most of the growth and size parameters and it was therefore included in all analyses. We also included the laying order*paternity, laying order*sex and paternity*sex interactions in our initial models. Because being laid sixth may have different effects in different-sized clutches, we ranked each nestling in one of the following five categories: hatched from the first, second, middle, penultimate or last laid egg. See, for example, Magrath et al. (2003) and Rosivall et al. (2005) for similar groupings.

We investigated posthatching performance of the young by analysing the effect of the above variables on measures of body size (tarsus length, body mass, feather length) and body condition on day 14 (just before fledging), and also on feather growth rate and body mass change during growth. As year had a significant effect on feather length at fledging (Rosivall et al. 2005), we controlled for year when analysing feather length patterns (but not in other analyses). Body condition of the chicks was estimated as the residual of body mass on tarsus length. Feather length of the nestlings increased linearly during the study period, so we used the slope of a linear regression to describe feather growth rate. In the case of body mass growth, we used body mass as the dependent variable and nestling age (2–12 days) as a repeated measure variable. The interactions of age with other variables were also included in the model. Significant effects for age interactions indicated that the given variables affected nestling growth.

We investigated the speed of embryonic growth by analysing the hatching time of the young (i.e. the time elapsed between the first hatching in a brood and the hatching of the chick in question). When controlled for laying order, this value should clearly show whether there is any difference between the development rate of extrapair and within-pair embryos. With a larger data set, the brood size*year*laying order interaction affected hatching time of the nestlings, and therefore this interaction was also included in the hatching time analysis (but not in other analyses).

In all the analyses described above, nonsignificant variables (except those background variables that were significant on a larger data set, see above) were deleted from the models one by one starting with the highest order interactions. (Inclusion of the above-mentioned nonsignificant background variables did not change the results qualitatively.) For these analyses we used the SAS 8.2 program (SAS Institute Inc., Cary, NC, U.S.A.). Nestling mortality was not analysed, because in broods where we had data on paternity, only four nestlings/embryos died.

When we investigated the effect of paternity on nestling body condition, the Hedges-corrected Cohen's *d* effect size was calculated using the calculator at <http://davidakenny.net/meta.htm>. The 95% confidence interval (CI) of this estimate was calculated by a jackknife procedure (Sokal & Rohlf 1981). Our estimate for the 95% CI is very conservative, because full broods, not nestlings, were ignored in the analyses during the jackknife procedure.

When testing the effect of laying order on sex and paternity of the offspring, we compared the observed versus expected number of male/extrapair young in different positions using a chi-square test. The effect of paternity on offspring sex was tested using generalized linear mixed models (glimmix macro), with brood identity as a random factor.

Analyses of Parental Trait Data

When we investigated the effects of parental traits on paternity of the broods, we used some additional data collected in 2004. If a parent was breeding in multiple years, it was entered in our analysis only once. Only broods of monogamous males and the primary broods of polygynous males were included in our analysis

(the exclusion of polygynous males did not change the results). So the sample size in this analysis was 61 broods. To analyse our data, we used generalized linear models with binomial error and logit link. Because the dispersion parameter was larger than 1.0, we tested the significance of parameters with *F* tests (Crawley 1993; Krackow & Tkadlec 2001; the *d*scale option was used in SAS 8.2). Nonsignificant terms were removed from the model using a backward stepwise deletion procedure.

Ethical Note

Trapping, ringing and blood sampling of birds were conducted according to protocols established during the long-term monitoring of the study population of collared flycatchers since the early 1980s. Adult birds were trapped with spring traps attached to the nestbox entrance and removed within a few minutes of trapping. The birds were released immediately after measurements and resumed breeding activities soon thereafter. Measuring nestling size every other day apparently had no adverse effect on the nestlings, because fledging success in the experimental nests was similar to that in unmanipulated nests. Work at the study site was done under permits from Duna-Ipoly National Park.

RESULTS

A large percentage (55.74%) of the broods contained extrapair young. Altogether, 20.61% of the nestlings were sired by extrapair fathers. None of the traits of the social mate (forehead patch size, wing patch size, body size and condition) predicted the females' participation in EPCs (Table 2). The timing of breeding and female body condition also showed no relationship with the paternity of the broods. However, the broods of large females were less likely to contain extrapair young than those of small females (Table 2, Fig. 1).

The embryonic development of extrapair young was not faster than that of their half sibs as indicated by the lack of difference in hatching time (Table 3), nor did they perform better after hatching (Table 3). Extrapair young did not differ in body mass and feather growth from their half sibs. Furthermore, nestlings fledged with the same size (body mass, tarsus length, feather length) and body condition independent of paternity. In contrast, in a Swedish study (Sheldon et al. 1997a), paternity had a significant effect on nestling body condition. To investigate the difference further, we estimated effect size in both studies. In the Swedish study, effect size was 0.36, which is outside of the 95% CI (0.23–0.32, mean 0.28) of our effect size, so we can be fairly sure that the two studies differed not only in their statistical significance but also in effect size, the effect size being smaller and nonsignificant in our study.

In broods with mixed paternity, the occurrence of extrapair young was independent of laying order ($\chi^2_4 = 3.41$, $P = 0.491$; Fig. 2). The sex of the extra- and within-pair young did not differ (proportion of males for EPY = 0.453, for WPY 0.441; $F_{1,84.5} = 0.01$, $P = 0.922$).

Table 2
The effect of parental traits on paternity of broods

Parental trait	<i>F</i>	<i>df</i>	<i>P</i>
Female tarsus length	7.32	1, 59	0.009
Male wing patch size	0.29	1, 58	0.589
Female body condition	0.30	1, 56	0.583
Male body condition	0.26	1, 55	0.615
Male forehead patch size	0.13	1, 54	0.721
Laying date	0.02	1, 53	0.881
Male tarsus length	<0.01	1, 52	0.967

The significant variable retained in the final model is in bold. Values indicated for nonsignificant terms are derived from the last model in which the given variable was included during the backward stepwise model selection.

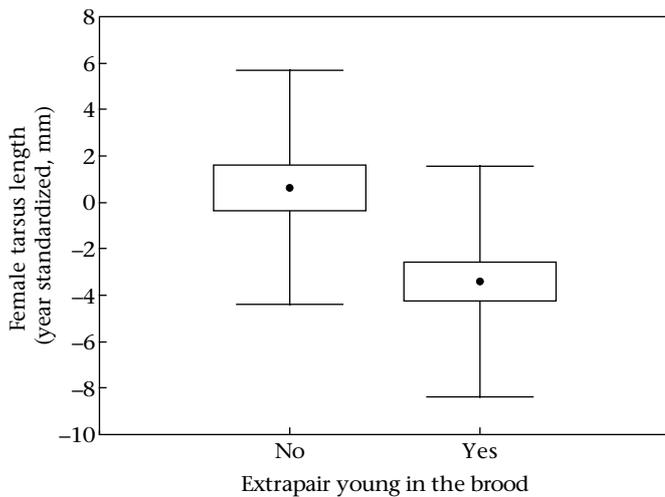


Figure 1. The relationship between female body size and paternity of the broods. Mean \pm SD (whiskers) and SE (boxes) are indicated.

As paternity did not affect any of the measures of offspring performance, we repeated all analyses with the inclusion of broods of genetically monogamous pairs when we analysed the effect of sex on nestling growth and size ('all broods' in Table 3). Although we found no sex difference in the hatching time of male and female nestlings (indicating that they developed at the same speed until hatching), male nestlings gained body mass faster after hatching as indicated by the effect of the interaction of sex and age on body mass (Fig. 3, Table 3). By the time of fledging, the sex difference in body mass had disappeared. However, the tarsus was significantly longer in females than in males (Fig. 4, Table 3), although the mean difference was only 0.7%. Since we estimated nestling body condition as the residual of body mass on tarsus length, females seemed to be in worse body condition on day 14. Although males tended to have faster feather growth than females, this difference was not significant and there was no sex difference in feather length at fledging (Table 3). The sex of the young was independent of their place in the laying order ($\chi^2_4 = 3.41$, $P = 0.491$).

DISCUSSION

Our results contradict previous findings concerning the role of a sexually selected character in extrapair mate choice at the same

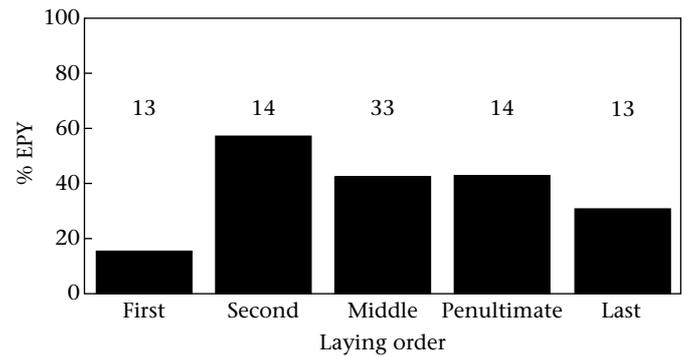


Figure 2. The percentage of extrapair young in relation to laying order in mixed-paternity broods. Number of chicks analysed is indicated above each bar (see Methods for the laying order groups).

study site. Michl et al. (2002) came to the conclusion that female collared flycatchers mated to males with a large forehead patch were less likely to participate in extrapair copulations. In contrast, in our study forehead patch size of the males was not related to the paternity in their broods. Neither was paternity related to the wing patch size (another secondary sexual character), body size and body condition of the males. Although we have no information on song characteristics of the males, which may also indicate their quality and may be correlated with paternity (Garamszegi et al. 2004a), the observed pattern suggests that the participation of females in EPCs was independent of the quality of their mates. This suggestion is also supported by the fact that extrapair young did not differ from their half sibs in any measures of performance. Nestlings grew at the same rate (both before and after hatching) and fledged with the same size and body condition independent of their genetic origin. If only those females that had poor-quality social mates engaged in EPCs, we would have expected to find differences in offspring performance, as reported previously in a Swedish population of collared flycatchers. In the Swedish population, extrapair young fledged in better condition than their within-pair half sibs (Sheldon et al. 1997a). However, we cannot completely exclude the possibility that females obtained good genes for their young, because the difference between EPY and WPY may be environment dependent (Garvin et al. 2006).

The question arises why different studies in the same study plot came to different conclusions. Although the sample size was moderate in the earlier study (Michl et al. 2002) because of

Table 3
The effect of paternity and sex on nestling growth and size

	Hatching time (approximating embryonic growth)			Body mass growth			14-day body mass			14-day tarsus length			14-day body condition			Feather growth			14-day feather length		
	F	df	P	F	df	P	F	df	P	F	df	P	F	df	P	F	df	P	F	df	P
Mixed-paternity broods																					
Laying order	65.80	4, 56	<0.001	3.03	20, 467	<0.001	0.22	4, 64	0.925	1.63	4, 65	0.177	0.90	4, 64	0.467	1.57	4, 58	0.196	13.34	4, 66	<0.001
Sex	0.83	1, 54	0.366	2.04	5, 460	0.071	0.78	1, 68	0.382	3.94	1, 69	0.051	3.40	1, 69	0.069	0.23	1, 57	0.631	0.78	1, 64	0.380
Laying order*sex	1.59	4, 50	0.191	0.49	20, 401	0.969	1.53	4, 60	0.204	0.10	4, 55	0.983	1.52	4, 60	0.208	0.19	4, 47	0.943	1.38	4, 60	0.251
Paternity	1.32	1, 55	0.255	0.69	5, 446	0.632	0.96	1, 69	0.331	0.20	1, 64	0.658	1.60	1, 68	0.210	0.01	1, 56	0.917	1.47	1, 65	0.230
Laying order*paternity	0.72	4, 46	0.580	1.37	20, 426	0.132	0.97	4, 56	0.433	0.56	4, 59	0.695	1.56	4, 56	0.199	0.54	4, 52	0.709	0.43	4, 56	0.788
Paternity*sex	0.03	1, 45	0.855	1.50	5, 421	0.190	0.01	1, 55	0.912	1.55	1, 63	0.217	0.14	1, 55	0.712	0.00	1, 51	0.964	0.00	1, 55	0.955
All broods																					
Laying order	96.55	4, 122	<0.001	7.89	20, 939	<0.001	1.14	4, 128	0.340	2.15	4, 120	0.079	0.19	4, 119	0.943	1.52	4, 105	0.202	28.89	4, 121	<0.001
Sex	0.57	1, 121	0.450	3.41	5, 939	0.005	1.57	1, 132	0.213	5.64	1, 124	0.019	4.21	1, 123	0.042	3.76	1, 109	0.055	1.24	1, 120	0.268
Laying order*sex	0.27	4, 117	0.896	1.05	20, 915	0.404	0.17	4, 124	0.951	0.26	4, 116	0.903	0.15	4, 115	0.964	0.06	4, 101	0.993	1.80	4, 116	0.133

Significant variables retained in the final model are in bold. Background variables other than laying order (see Methods) are not indicated. Values indicated for nonsignificant terms are derived from the last model in which the given variable was included during the backward stepwise model selection. Note that in the case of body mass growth where we used a repeated measure approach, all effects are interactions with age (e.g. 'laying order' in the table refers to 'laying order*age'), because these interactions show whether the given variable (e.g. 'laying order') had an effect on body mass growth.

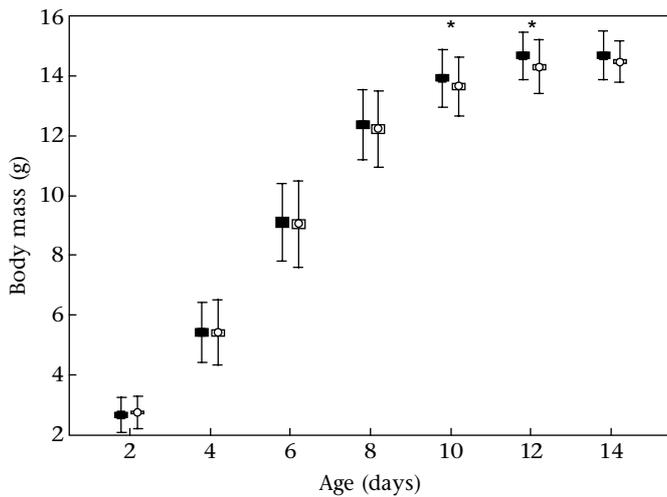


Figure 3. The effect of sex on nestling growth. Asterisks indicate significant difference in body mass between males (black box) and females (open box) in post hoc tests performed for the age categories separately. Mean \pm SD (whiskers) and SE (boxes) are indicated.

methodological constraints, and thus statistical artefact as an explanation cannot be excluded, methodological differences between the studies raise an exciting possibility. It is clear from our results that even the first egg could contain an extrapair embryo (Fig. 2) and thus that females could copulate with nonpair males before starting egg laying. Prelying copulations with nonpair, non-neighbouring males have been suggested in other species too (Dunn et al. 1994). These copulations could have happened before mate choice (when females were visiting multiple male territories) or after mate choice. In the first case, females would have no knowledge of their future social mate, so mate quality-independent 'extrapair' copulations are expected. There could be two reasons for the participation of females in copulations before mate choice: (1) males may be able to force females to copulate with them because they are not yet guarded; or (2) females may actively solicit copulations to gain different benefits without risking reduced paternal care. These benefits may involve, for example, fertility insurance (Sheldon 1994; Gray 1997), compatible genes (Johnsen et al. 2000; Foerster et al. 2003) or increased genetic variability of the offspring (Williams 1975; Westneat et al. 1990); for a review see Griffith et al.

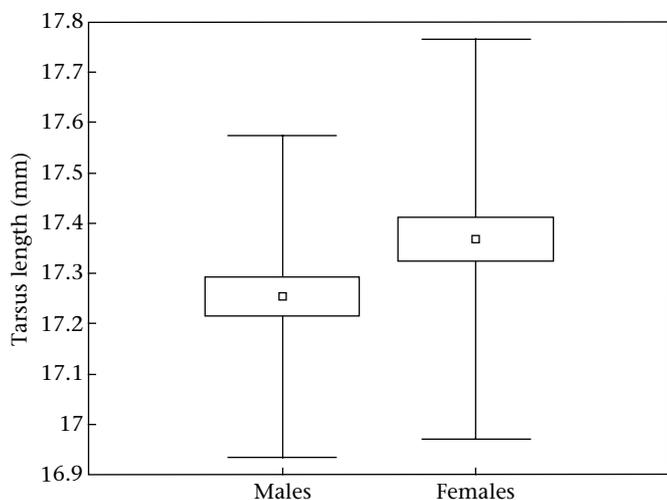


Figure 4. Sex difference in nestling tarsus length on day 14. Mean \pm SD (whiskers) and SE (boxes) are indicated.

(2002). Anyway, if many females participate in male quality-independent EPC before mate choice but only those females that end up with a low-quality male, continue the pursuit of EPCs after mate choice, different investigation methods may come to different conclusions. Michl et al. (2002) detected EPCs by an increase in sperm number on the perivitelline layer of subsequent eggs (note that sperm transfer by the social mate was prevented, so the increase was clearly indicative of EPC). Therefore they could detect EPCs only during egg laying and these EPCs were dependent on the male quality. However, sperm from pre-mating copulations may survive until egg laying and result in extrapair young, so paternity analysis of nestlings may show that EPCs are independent of male quality.

While the above hypothesis may explain the difference found within the same study plot using different methods, differences between studies using the same method (Sheldon & Ellegren 1999; Garamszegi et al. 2004a; Krist et al. 2005; present study) are hard to explain. The two studies that found a lower percentage of mixed-paternity broods (Sheldon & Ellegren 1999; Garamszegi et al. 2004a; 32.9% and 30.6%, respectively) also suggested that male quality has a role in EPCs, while the two studies with a higher percentage of mixed-paternity broods (Krist et al. 2005; present study; 51.9% and 55.74%, respectively) came to the opposite conclusion. Recent studies suggest that both EPC patterns and the effects of paternity can depend on the environment (Johnsen & Lifjeld 2003; Garvin et al. 2006). Such effects have the potential to explain population differences and should be taken into account in future studies.

The role of female characteristics in extrapair copulations has received little attention. The constrained female hypothesis (Mulder et al. 1994; Gowaty 1996) suggests that females that need less help from their social mate in rearing the chicks are more likely to risk reduced care as a cost of extrapair matings. Although in some species the assumption of this hypothesis (i.e. male care is positively related to the certainty of paternity) is not fulfilled (Wagner et al. 1996; Kempnaers et al. 1998; Peterson et al. 2001), in others, including the collared flycatcher, the assumption is supported (Wright & Cotton 1994; Sheldon et al. 1997b; Lifjeld et al. 1998; Sheldon & Ellegren 1998). So one might expect that good-quality females are more likely to have extrapair young. Male preference for high-quality females in extrapair matings would also result in such a pattern. However, our results show that larger females (suggested to be of better quality; Garamszegi et al. 2004c) were less likely to participate in extrapair copulations. If extrapair copulations (or pre-mating copulations) are mainly due to males forcing unguarded females to copulate (Clutton-Brock & Parker 1995), the pattern could be explained by larger females being more successful at counteracting these attempts. Alternatively, small, low-quality females may benefit more from extrapair copulations; however, it is unclear how, because extrapair young did not perform better than within-pair young.

Although the primary goal of this study was to investigate the factors that determine paternity of collared flycatcher broods and the effect of paternity on offspring performance, we also included offspring sex in the latter analyses as it may confound the observed growth patterns for the following reasons. First, females may manipulate the sex of their offspring in relation to paternity, if paternity of an offspring is predictable, for example on the basis of laying order. Second, even in sexually size-monomorphic species males and females may grow at different rates (Martins 2004). We found that the paternity of the young was not related to laying order. Moreover, similarly to previous results from a Swedish population (Sheldon & Ellegren 1996), the sex ratio of extra- and within-pair young did not differ. However, male nestlings gained weight faster than females, although females had caught up in body mass by day 14. We found a similar tendency for feather growth. In

the Swedish population, growth rates were not measured, but males had longer wings before fledging (Sheldon et al. 1998), perhaps indicating faster male growth. Surprisingly, on day 14 the tarsus of the females was longer than that of males in our population. This apparent contradiction may be explained by the different developmental states of the sexes. Our body mass growth data imply that male nestlings grew faster, suggesting that on day 14 sons were more developed. The tarsus length of the nestlings decreases slightly after it reaches its maximum, probably because of water loss from the tissues. If males reach this phase of development faster, their tarsus may appear to be smaller and consequently the estimate of female condition would be systematically lower than that of males (a similar sex difference in body condition was found in Krist et al. 2004, but not in Sheldon et al. 1998). Indeed, in a small subset of the chicks where we measured tarsus length during development, the change in tarsus length between day 14 and the day when the tarsus was longest prior to day 14 was more negative in males than in females (males = -0.604% , $N = 23$; females = -0.178% , $N = 26$). The difference (0.426%) is rather close to the difference observed between the tarsus length of males and females on day 14 (0.7%). This result clearly shows that caution has to be taken when using the residual body mass as an estimate of body condition in developing young, because it may primarily be determined by the developmental state of the offspring.

Our results on sex-dependent growth rates have other implications too. In a previous study on sex ratio adjustment in collared flycatchers, we showed that females produced male-biased brood sex ratios late in the season (Rosivall et al. 2004). We then hypothesized that this pattern could be adaptive if male nestlings perform better late in the season. For example, faster development of males may be beneficial because this allows for earlier fledging. On the other hand, faster development may require more resources and result in developmental failures when food is scarce. Further studies should clarify whether sexual differences in growth rate depend on rearing conditions and explain the observed sex ratio pattern, as has been done in the zebra finch, *Taeniopygia guttata* (Kilner 1998; Martins 2004).

In summary, our results show that paternity was not related to male quality in a Hungarian population of collared flycatchers. As a consequence, extrapair young did not grow faster or fledge in better condition. However, we found that female quality in terms of body size was related to paternity. While we can only speculate about the explanation of this result, it clearly shows that the role of female quality in EPCs deserves more attention. Previous results in the same and in other collared flycatcher populations show that extrapair paternity patterns may differ considerably between studies probably because of environmental factors. In addition, our results also suggest that different extrapair copulation strategies may be present at different stages of the female reproductive cycle. These issues should be investigated further. Although extrapair paternity was not related to nestling growth patterns, growth was sex dependent so that male nestlings grew faster. Because biased brood sex ratios are often observed in birds, we argue that sex-biased development should be taken into account in studies using nestling growth or condition as measures of nestling quality.

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