

1 Laying date and polygyny as determinants of annual reproductive success in male collared
2 flycatchers (*Ficedula albicollis*): a long-term study

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18

19 **Abstract**

20 Annual reproductive success (ARS) is one of the main components of lifetime reproductive
21 success, a reliable measure of individual fitness. Previous studies often dealt with ARS and
22 variables potentially affecting it, but the majority of them treated only one or two factors at
23 the same time and long-term studies are scarce. Here we used an 18-year dataset to quantify
24 ARS of male collared flycatchers (*Ficedula albicollis*) on the basis of recruited offspring. We
25 simultaneously assessed the effect of start of breeding, age, polygyny, body size and the
26 expression of forehead patch (a sexually selected trait). Males that bred around the yearly
27 median breeding date had the highest ARS, while both early and late birds were
28 disadvantaged. Polygynous males were more successful in years with good food supply, while
29 in years with low food availability they did not have more recruits than monogamous males.
30 The age of males, their forehead patch size and body size did not affect the number of
31 recruits. Our findings support the importance of breeding date, and suggest stabilizing
32 selection on it in the long term. We also show that polygyny is not always advantageous for
33 males, and its fitness payoff may depend on environmental quality.

34

35

36 **Key-words**

37 timing of reproduction, fecundity, life-history, mating status, year-quality

38 **Introduction**

39 Annual reproductive success (ARS) is one of the most important variables in the life-history
40 of individuals, as, beside lifespan, it is the main determinant of lifetime reproductive success.
41 It is difficult to select the most important among the factors presumably influencing the rate
42 of annual offspring production, but the morphological characteristics of individuals, their age,
43 timing of reproduction and mating status (polygynous or monogamous) may often play
44 important roles.

45

46 Age is a frequent subject of ecological studies (Clutton-Brock 1988; Newton 1989; Forslund
47 and Pärt 1995). Most studies suggest that reproductive performance increases with age early
48 in life (Forslund and Pärt 1995; Pärt 2001). However, in some species the reproductive
49 performance of old and young individuals did not differ (Wendeln and Becker 1999) or young
50 individuals reached an even higher success (Lamprecht 1990; Descamps et al. 2006). The
51 latter can mainly occur in species in which there is a significant variance in age of first
52 reproduction, and only individuals of high quality are able to reproduce at a younger age
53 (Descamps et al. 2006).

54

55 In seasonal habitats, breeding conditions change during the reproductive season, so the
56 appropriate timing of breeding can increase reproductive success. This is especially widely
57 known in birds. Several studies have focused on the seasonal decline of reproductive success
58 and interpreted this pattern as the outcome of decreasing food supply during the breeding
59 season or differences in quality between early and late breeders or their territories (reviewed
60 by Verhulst and Nilsson 2008). However, breeding too early may not be favourable either, as
61 in early spring the amount of available food is still quite low. In this case we expect that
62 breeding success will increase first and then decrease later in the breeding season, showing a

63 polynomial curve overall. Such non-linearity, however, has been investigated in only a few
64 studies (e.g. Brinkhof et al. 1993). Moreover, studies dealing with the seasonal decline
65 estimated reproductive success predominantly as fledging success, and reproductive success
66 estimated by recruitment has been used mainly in resident species (Verhulst and Nilsson
67 2008). However, the seasonal pattern of recruitment can be different between resident and
68 migratory birds, as migration strongly constrains arrival at the breeding site and the initiation
69 of breeding (Both and Visser 2001).

70

71 ARS can be affected by individual characteristics such as body size (Grant and Grant 2000) as
72 well as sexually selected traits (Gustafsson et al. 1995; Hasselquist et al. 1996) that can reflect
73 individual quality. Individuals with more elaborate sexual traits often perform better (Møller
74 1994; Hasselquist et al. 1996) and females may often choose more ornamented males to
75 acquire benefits for themselves and for their offspring. Hence, males with more elaborated
76 traits usually realize higher mating and reproductive success (Gustafsson et al. 1995; Kruuk et
77 al. 2002).

78

79 In facultatively polygynous species, males can also increase their reproductive output by
80 acquiring a second female. However, in birds, the advantage of polygynous males is not so
81 obvious when considering the recruitment rate of offspring to the breeding population
82 (Lubjuhn et al. 2000; Pribil 2000; Herényi et al. 2012). Males cannot feed two broods at the
83 same intensity as only one brood, which results in lower fledging condition at least in the
84 secondary brood of polygynous males. This reduces the chance of fledglings to return in
85 following years (Lindén et al. 1992; Both et al. 1999). It may occur that polygynous males
86 become more successful than monogamous males only in certain years. Environmental
87 conditions such as food availability can considerably influence the success of polygyny, since

88 in the case of rich food supply nestlings will suffer less from reduced paternal care. If
89 environmental conditions are strongly variable among years, then the reproductive success of
90 monogamous and polygynous males may be similar in the long-term, despite the situation-
91 specific advantages of the polygynous strategy.

92

93 Although individuals' reproductive success is one of the main subjects of life-history
94 research, long-term studies are scarce (Clutton-Brock and Sheldon 2010). In most cases, data
95 of one or two years have been analysed (e.g. Siikamäki 1998; Daunt et al. 1999), but
96 conclusions based on such datasets are not entirely reliable, since environmental conditions
97 may strongly differ among years. One of the main disadvantages of short-term studies is that
98 reproductive success can only be determined by clutch size or the number of fledged young.
99 However, the number of recruits gives a much more accurate estimate of individuals'
100 reproductive success as it also considers the period between reaching independence and the
101 first reproduction.

102

103 In this long-term study we simultaneously investigated the effect of age, breeding date and
104 mating status, as well as body size and the size of the sexually selected forehead patch on the
105 ARS of male collared flycatchers (*Ficedula albicollis*). We estimated ARS as the number of
106 recruits. The independent variables we used are rarely investigated simultaneously, and our
107 aim was to assess their relative contributions to variation of reproductive success. In addition,
108 as a previous study showed that environmental conditions are highly variable in our study
109 area (Török et al. 2004), we also studied the effect of year-quality as determined by food
110 availability.

111

112

113 **Materials and methods**

114 *Study species and field methods*

115 The collared flycatcher is a small, long-distance migratory, hole-nesting, insectivorous
116 passerine breeding in deciduous woodlands of Central Europe and wintering in sub-Saharan
117 Africa. This species is ideal for long-term studies of reproductive success as it prefers
118 nestboxes, can be captured easily, and has high breeding site fidelity (Pärt and Gustafsson
119 1989; Könczey et al. 1992; Hegyi et al. 2002) and considerable local recruitment rates (Pärt
120 1990; Török et al. 2004). Our data were collected between 1988 and 2005 in Pilis Mountains,
121 Hungary (47°43' N, 19°01' E), in an oak-dominated forest, where more than 750 nestboxes
122 were placed. Collared flycatcher males arrive at our nestbox plots in early or mid April and
123 females a few days later. Nestboxes were checked multiple times a week during the whole
124 nesting period, so breeding attempts were followed from nest building to fledging. Most
125 parents were captured and ringed when feeding young. Capture effort was high throughout.
126 The size of males' white forehead patch was estimated as a product of maximum height and
127 maximum width. Forehead patch dimensions and tarsus length (to estimate body size) were
128 measured with a calliper to the nearest 0.1 mm. Systematic differences among measurers were
129 corrected for based on mean tarsus and forehead patch values taken in the same seasons. The
130 age of males was determined based on ringing data or by plumage colour (Török et al. 2003).
131 Start of breeding was defined as the day when the first egg of a clutch was laid. Nestlings
132 were ringed after the age of eight days. The collared flycatcher is predominantly
133 monogamous, but a fraction of males successfully attract two females and become
134 polygynous. During the study period, we observed 117 polygynous individuals out of 2055
135 breeding males (5.7 %).

136

137 Year-quality was determined by the availability of lepidopteran larvae, an important
138 component of the nestling diet of collared flycatchers (Török 1986), estimated on the basis of
139 caterpillar frass mass (Zandt et al. 1990). Caterpillar frass was collected in fifteen 0.25 m²
140 trays, which were emptied at three to six day intervals. Rains and other accidents resulted in a
141 varying number of samples per collection period. Year-quality was determined using the
142 amount of caterpillar frass production at the study plot in the 15 days with the highest frass
143 mass in each year divided by the number of collectors.

144

145 *Statistical analyses*

146 For analysing ARS an 18-year dataset was used. Individuals that were subject to experiments
147 that could have influenced their breeding success were excluded. Breeding attempts in which
148 data of males were not complete were also excluded from the analyses. After these omissions
149 our dataset contained data of 1061 breeding attempts of 796 male flycatchers. Of those 1061
150 breeding attempts males simultaneously fathered two broods in 41 cases. If there was more
151 than one measurement from an individual in a given year, one of them was selected randomly.
152 There was a significant relationship between age and forehead patch size, so to avoid
153 multicollinearity, age-standardized forehead patch size was used in the analyses. Age was
154 used as a four-level categorical factor with category 4 comprising all males older than three
155 years.

156

157 The ARS of males was characterized by the number of recruits (offspring that became
158 members of the reproductive population). As a significant proportion of recruits return only at
159 the age of two or three, males that bred after the year 2002 were excluded from the analyses,
160 as their recruits may have returned after 2005, the end of the study period. A male was
161 considered polygynous if it was caught in two nestboxes while feeding nestlings. It was

162 possible that in some cases polygyny could not be detected, so the observed rate of polygyny
163 is an underestimate. Given the high capture effort, polygynous males caught at only one nest
164 probably allocated nearly all of their care to this nest (included here as a monogamous nest)
165 while neglecting the other nest (not used here due to the lack of the male). A secondary brood
166 without the male caring for the offspring presumably produces little reproductive output, so
167 the misclassification of these birds as monogamous is likely to bias estimated polygynous
168 ARS upwards.

169
170 Laying date was entered in the models as a deviation from the annual median within each age-
171 category, thereby controlling for age differences and environmental variation between years.
172 As this year- and age-standardized laying date was not normally distributed, $\log(x + \min(x) +$
173 $1)$ transformation was performed on laying date data, where $\min(x)$ is the smallest relative
174 value in the whole dataset. For including both linear and squared terms of laying date in the
175 models, this variable was centred (by subtracting the sample mean from all values) before
176 fitting the models as suggested recently (Schielzeth 2010).

177
178 For analysing data generalized linear mixed models with restricted maximum likelihood
179 parameter estimation and Poisson error were used as implemented in the GLIMMIX macro of
180 SAS 9.1 (SAS Institute, Cary, NC). Patterns of ARS were analysed using the number of
181 recruits a male produced in the given year as a dependent variable, age and mating status as
182 factors, year-quality, tarsus length, forehead patch size, laying date and squared laying date as
183 covariates and year and male identity as random factors. All two-way interactions with year
184 type were also calculated. Patterns of ARS were also estimated separately in good years and
185 in bad years (when caterpillar frass mass was above or below the average, respectively).
186 Using clutch size correction did not change the results. In all models, a backward stepwise

187 model selection procedure was used and results reported here for nonsignificant terms reflect
188 their reintroduction to the final model one by one.

189

190

191 **Results**

192 Male collared flycatchers produced at least one recruit in one third of yearly breeding
193 attempts (33.8 %). The maximum number of recruits of a male produced in a year was five.
194 Correlates of ARS are presented on Table 1. The ARS of males was significantly related to
195 breeding date. Both linear and squared terms had a negative effect on the number of recruits,
196 with nests close to the median laying date being the most successful (Fig. 1). The age of
197 males was not associated with their reproductive success. Morphological variables did not
198 seem to influence ARS, as there was no relationship between the number of recruits and
199 tarsus length or the size of the forehead patch. With respect to the mating status of birds, a
200 significant interaction was detected between year-quality and polygyny. Other interactions
201 were non-significant.

202

203 As year-quality-interactions were found with mating status, data were also analysed for good
204 and bad years separately. The number of recruits was influenced by mating status in years
205 with high food supply, with polygynous males having more recruits than monogamous males
206 (Table 2, Fig. 2). In years with low food availability, however, there was no significant effect
207 of polygyny on ARS (Table 2, Fig. 2). It seems that the success of polygynous males was
208 reduced in bad years (Fig. 2, but the difference is not significant), whereas that of
209 monogamous males practically did not change (Mann–Whitney U-test for polygynous males:
210 adjusted $Z = -1.665$, $p = 0.096$, $n_{\text{good}} = 25$, $n_{\text{bad}} = 16$; for monogamous males: adjusted $Z =$
211 0.113 , $p = 0.910$, $n_{\text{good}} = 605$, $n_{\text{bad}} = 415$).

212

213

214 **Discussion**

215 The reproductive success of early breeders is often higher than that of late breeders. This is a
216 generally accepted pattern that has been found in numerous studies. Reasons for this include
217 seasonally decreasing food supply (Perrins 1970; Siikamäki 1998), decreasing territory
218 quality (Potti and Montalvo 1991a), better chance to breed twice when starting early in the
219 season (Saino et al. 2004), seasonally increasing probability of being cuckolded (Johnson et
220 al. 2002), increasing density of already fledged young (Tinbergen et al. 1985), decreasing
221 time for fledglings before migration (Dawson and Clark 2000) or increasing moult-breeding
222 overlap (Svensson and Nilsson 1997; Siikamäki 1998). Finally, predation pressure may also
223 increase with breeding date (Götmark 2002; but see Hartley and Shepherd 1994; Burger et al.
224 1996). The disadvantages of breeding too early have received much less attention than those
225 of breeding too late, though harsh weather early in the season may be costly for breeding
226 birds and may limit food availability for egg production (Perrins 1970; Nilsson 1994; Brown
227 and Brown 2000).

228

229 Our data suggest that birds starting late in the breeding season produced no or very few
230 recruits, but the reproductive success of individuals breeding too early was also low, and birds
231 that generally bred near the yearly median had the highest number of recruited offspring. A
232 polynomial seasonal trend in reproductive success has been revealed in only a few studies
233 (Brinkhof et al. 1993; Lepage et al. 2000). Such a pattern can evolve for various reasons.
234 First, we can suppose that there is an optimal time window when starting breeding is
235 profitable. The majority of birds lay at this period, but there are always individuals that breed
236 earlier or later. The reason for this can be that they cannot estimate the optimal initiation time

237 well, arrive too late from the wintering ground, or cannot mate in time e.g. because they are
238 inferior males. Second, if the environmental conditions vary between years (as in our
239 population, see Török et al. 2004) this may result alternating selection on laying date, that is,
240 in one year it is advantageous to breed early, while in another year, breeding late is more
241 rewarding (Brown and Brown 2000). Flycatchers have little opportunity to optimize the
242 timing of breeding, as migration and the date of arrival are also very important constraints for
243 them (Both and Visser 2001). Finally, a polynomial trend can evolve if individuals breed in
244 synchrony with conspecifics. The advantages of synchronous breeding can be improved
245 defence, dilution of predation pressure (Hatchwell 1991), or more opportunity for proper mate
246 choice as the more birds breed together, the larger is the subset of potential mates they can
247 sample. However, in our case, synchronous breeding may be an unlikely reason, as an earlier
248 study suggested that higher density in the breeding area negatively influenced the hatching
249 and fledging success of collared flycatchers (Török and Tóth 1988).

250

251 Age of male collared flycatchers did not explain their number of recruits. This finding is in
252 contrast to the usually revealed relationship that reproductive success increases with age
253 (Forslund and Pärt 1995; Catry and Furness 1999; Daunt et al. 1999; Pärt 2001). In many
254 cases the major difference in age-specific reproductive success occurs between the youngest
255 and the older breeders (Daunt et al. 1999; Pärt 2001). However, some studies found similarly
256 no association between male age and reproductive success (Wendeln and Becker 1999;
257 Robertson and Rendell 2001). It is possible that despite all individuals trying to start breeding
258 at younger ages, only high-quality individuals succeed in doing so (Harvey et al. 1985; Pärt
259 1995). Indeed, in certain species, including flycatchers, some yearling individuals skip
260 breeding, while others rear offspring at this age (Potti and Montalvo 1991b; Robertson and
261 Rendell 2001; Cooper et al. 2009), and this could also be true for our collared flycatcher

262 population as a significant proportion of males (60.9 %) breed first when they are two years
263 old. The higher quality of yearling breeders could counterbalance the higher breeding
264 experience of older breeders, and yearlings could reach similar (or even higher) reproductive
265 success than older individuals.

266

267 The lack of age effect on ARS could also be explained if females compensate the
268 inexperience of their mates when mate with a yearling male. This can appear as laying fewer
269 eggs (Pyle et al. 1991; our unpublished data), which results in fewer fledglings but in better
270 condition (Gustafsson and Sutherland 1988). Another possibility if they allocate higher
271 amounts of some beneficial compounds (e.g. testosterone) to the eggs (Schwabl 1996; Eising
272 et al. 2001), which has indeed been found in our population (Michl et al. 2005).

273

274 The size of the white forehead patch of male collared flycatchers did not influence the number
275 of recruits. This is surprising considering that forehead patch size is a sexually selected trait in
276 our population: males with a larger patch acquire a female earlier, even relative to their own
277 arrival date (Hegyi et al. 2010). On the other hand, our results are in agreement with those of
278 earlier studies performed in this population, suggesting that this trait is a poor indicator of
279 genetic or phenotypic quality in our birds (Garamszegi et al. 2006; Hegyi et al. 2002, 2006,
280 2007; Hargitai et al. 2012; but see Hegyi et al. 2011, Markó et al. 2011). Furthermore, in a
281 recent long-term study we showed that forehead patch size did not predict lifetime offspring
282 recruitment (Herényi et al. 2012). We can assume that the advantages of large forehead patch
283 may appear in other processes of sexual selection, such as extra-pair paternity. However,
284 previous studies investigating the relationship between forehead patch size and extra-pair
285 paternity found contradictory results (Michl et al. 2002; Rosivall et al. 2009). Therefore, the
286 exact advantages of wearing a large forehead patch have not been entirely clarified yet, and

287 long-term data on within- and extra-brood paternity would be helpful to further illuminate the
288 role of this trait.

289

290 In species with infrequent polygyny, polygynous males may gain considerable advantages
291 over monogamous males, as shown by many studies (Davies and Houston 1986; Soukup and
292 Thompson 1998). The disadvantages of polygyny, however, have been mainly investigated
293 from the females' viewpoint (Slagsvold and Lifjeld 1994; Huk and Winkel 2006), though the
294 difference between the reproductive success of polygynous and monogamous males may not
295 be very large in cases when reduced male help impairs the success of secondary or both
296 females (Slagsvold and Lifjeld 1994; Garamszegi et al. 2004). Here we found that there was
297 no difference between monogamous and polygynous collared flycatcher males in the number
298 of recruits, but the interaction between year-quality and mating status was significant.
299 Polygyny was advantageous in years with high food supply, while in years with low food
300 availability the advantage of polygynous males diminished and their success became similar
301 to that of monogamous males. This is in agreement with our previous result that polygyny did
302 not affect the lifetime reproductive success of male collared flycatchers (Herényi et al. 2012).
303 These findings raise the fundamental question of whether it is adaptive for males to build
304 polygynous partnerships. Based on the strength of the observed pattern we can suppose that
305 polygynous males produce more recruits only in years with high food availability, but males
306 may try to become polygynous every year, because they cannot predict food abundance early
307 in the breeding season (Lubjuhn et al. 2000). This explanation may easily apply to our
308 population, where the unpredictable fluctuations of food availability prevent even the
309 individual optimization of clutch size (Török et al. 2004). Certainly, polygynous males may
310 have gained some advantage that we could not measure, and which may even be independent
311 of year-quality, such as achieving extra-pair copulations (see next paragraph below). Fitness

312 benefits to polygynous males may also appear in the attractiveness of their offspring
313 (Gwinner and Schwabl 2005; Huk and Winkel 2006), which will increase the number of
314 grandoffspring. Although in this study we did not assess this variable, data from a Swedish
315 population of collared flycatchers suggest no reproductive advantage for the offspring of
316 polygynous males (Gustafsson and Qvarnström 2006).

317

318 Extra-pair paternity plays an important role in influencing the reproductive success of males
319 in many bird species. Unfortunately, we could not assess this component of reproduction
320 because we did not have blood samples from individuals for most years of the study period.
321 Given that paternity in the own nest is apparently not related to male ornaments, body size or
322 breeding time in our population (Rosivall et al. 2009; but see Michl et al. 2002) a directional
323 effect of extra-pair paternity on our results is unlikely in this respect. This may be true for
324 male age as well (see Krist et al. 2005). However, the relationship between paternity and
325 polygyny could be negative (Pilastro et al. 2002), very weak (Pearson et al. 2006) or positive
326 (Soukup and Thompson 1998) and data on flycatchers are scarce. Therefore, our data on
327 polygyny must be treated with caution. Studies conducted in different populations of the
328 sibling species pied flycatcher (*Ficedula hypoleuca*) consistently showed that polygynous
329 males had extra-pair young in their broods more frequently than monogamous males (Brün et
330 al. 1996; Lubjuhn et al. 2000; Drevon and Slagsvold 2005). These findings suggest that
331 considering extra-pair paternity would even further reduce the advantage of polygynous over
332 monogamous males. So, in an extreme case it would remove the benefit of polygyny even in
333 years with high food availability.

334

335 In conclusion, breeding date showed a polynomial relationship with offspring recruitment,
336 which emphasizes that the disadvantages of early breeding should also be considered when

337 studying the effect of timing. The age of collared flycatcher males did not influence their
338 ARS. Nor did the morphological characteristics of males (body size and forehead patch size),
339 which is in line with our earlier findings concerning lifetime reproductive success (Herényi et
340 al. 2012). In years with low food availability, there was no relationship between polygyny and
341 reproductive success, however, in years when food availability was high, polygynous males
342 produced more recruits than monogamous ones. These results show that several years should
343 be take into account when investigating the effect of mating status on reproductive success,
344 and one should consider food supply.

345

346

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354 Management.

355

356

357 **Ethical standards**

358 All capture and handling procedure complied with the current laws of Hungary, and were
359 approved by the appropriate authority.

360

361

362 **Conflict of interest**

363 The authors declare that they have no conflict of interest.

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365

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619

620 **Fig. 1**

621 The number of recruits in relation to laying date (mean \pm SE)

622

623 **Fig. 2**

624 ARS in relation to mating status in years with high (good years) and with low food supply

625 (bad years) respectively (mean \pm SE). Monogamous males: solid circles; polygynous males:

626 open circles. Sample sizes are given

627

628 Table 1
 629 Correlates of annual reproductive success of male collared flycatchers as estimated by the
 630 number of recruits.
 631 Generalized linear mixed models with restricted maximum likelihood parameter estimation,
 632 Poisson error and backward stepwise model selection (results for nonsignificant terms reflect
 633 their reintroduction to the final model one by one). n = 1061 (monogamous 1020, polygynous
 634 41)
 635

	df	F	p
Laying date	1, 211	42.95	< 0.001
Squared laying date	1, 211	13.40	< 0.001
Year-quality (YQ)	1, 211	3.40	0.067
Age	3, 208	0.83	0.481
Mating status	1, 211	2.87	0.092
Forehead patch size	1, 210	0.72	0.397
Tarsus length	1, 210	0.12	0.732
YQ x mating status	1, 211	8.07	0.005
YQ x age	3, 205	1.80	0.148
YQ x forehead patch size	1, 209	0.44	0.507
YQ x tarsus length	1, 209	0.40	0.529
YQ x laying date	1, 210	1.13	0.289
YQ x squared laying date	1, 210	0.07	0.792

636

637 Table 2
 638 Variables relating to annual reproductive success of male collared flycatchers in years with
 639 high and with low caterpillar food availability (good and bad years, respectively).
 640 Generalized linear mixed models with restricted maximum likelihood parameter estimation,
 641 Poisson error and backward stepwise model selection (results for nonsignificant terms reflect
 642 their reintroduction to the final model one by one). n = 431 (monogamous 415, polygynous
 643 16) for good years and n = 630 (monogamous 605, polygynous 25) for bad years
 644

	Good years			Bad years		
	df	F	p	df	F	p
Mating status	1, 58	6.86	0.011	1, 58	2.48	0.121
Laying date	1, 58	35.25	< 0.001	1, 59	16.21	< 0.001
Squared laying date	1, 56	2.72	0.105	1, 59	9.76	0.003

645