

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 m<sup>2</sup>  
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.

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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.

364

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
<b>Laying date</b>	<b>1, 211</b>	<b>42.95</b>	<b>&lt; 0.001</b>
<b>Squared laying date</b>	<b>1, 211</b>	<b>13.40</b>	<b>&lt; 0.001</b>
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
<b>YQ x mating status</b>	<b>1, 211</b>	<b>8.07</b>	<b>0.005</b>
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
<b>Mating status</b>	<b>1, 58</b>	<b>6.86</b>	<b>0.011</b>	1, 58	2.48	0.121
<b>Laying date</b>	<b>1, 58</b>	<b>35.25</b>	<b>&lt; 0.001</b>	<b>1, 59</b>	<b>16.21</b>	<b>&lt; 0.001</b>
<b>Squared laying date</b>	1, 56	2.72	0.105	<b>1, 59</b>	<b>9.76</b>	<b>0.003</b>

645