

1 **Aggressive behavior of the male parent predicts brood sex ratio in a songbird**

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16

17 **Abstract** Brood sex ratio is often affected by parental or environmental quality, presumably
18 in an adaptive manner that is the sex that confers higher fitness benefits to the mother is
19 overproduced. So far, studies on the role of parental quality have focused on parental
20 morphology and attractiveness. However, another aspect, the partner's behavioral
21 characteristics, may also be expected to play a role in brood sex ratio adjustment. To test this
22 hypothesis, we investigated whether the proportion of sons in the brood is predicted by the
23 level of territorial aggression displayed by the father, in the collared flycatcher (*Ficedula*
24 *albicollis*). The proportion of sons in the brood was higher in early broods and increased with
25 paternal tarsus length. When controlling for breeding date and body size, we found a higher
26 proportion of sons in the brood of less aggressive fathers. Male nestlings are more sensitive to
27 the rearing environment, and the behavior of courting males may often be used by females to
28 assess their future parental activity. Therefore, adjusting brood sex ratio to the level of male
29 aggression could be adaptive. Our results indicate that the behavior of the partner could
30 indeed be a significant determinant in brood sex ratio adjustment, which should not be
31 overlooked in future studies.

32

33 **Keywords** Attack latency; Collared flycatcher; Laying date; Male quality; Personality; Sex
34 allocation

35 **Introduction**

36 The brood sex ratio that provides maximal fitness benefit is expected to vary between females
37 when their individual physical, social and ecological conditions differently influence the fate
38 of male and female offspring. In such a case, selection should favor the ability of mothers to
39 adjust the sex ratio of their brood. According to the Trivers–Willard-hypothesis (Trivers and
40 Willard 1973), mothers in above-average body condition should produce male-biased broods,
41 whereas mothers in below-average body condition should produce female-biased broods,
42 whenever male reproductive success is more variable and hence more dependent on maternal
43 investment than female reproductive success. Indeed, such a pattern has been found in certain
44 bird species, for example in the tree swallow (*Tachycineta bicolor*) (Whittingham and Dunn
45 2000) and the house wren (*Troglodytes aedon*) (Whittingham et al. 2002). Moreover, brood
46 sex ratio has been shown to vary as a function of partner quality (e.g. ornament size in
47 Ellegren et al. 1996; body size in Kölliker et al. 1999; strophe bout length in Dreiss et al.
48 2006), breeding date (Daan et al. 1996) and territory quality (Appleby et al. 1997), factors
49 that, similarly to maternal condition, can affect future reproductive success of the offspring in
50 a sex-specific manner. Other hypotheses focus on the survival prospect of the offspring or the
51 mother because of differences in early sensitivity and energy demand between male and
52 female offspring (Cordero et al. 2000; Martins 2004; Addison et al. 2008; Rosivall et al.
53 2010). On the one hand, mothers breeding in poor body condition or an unfavorable
54 environment might overproduce the sex that is less susceptible to nutrient shortage, because it
55 has a greater chance to survive under such a condition (Kilner 1998; Nager et al. 1999). On
56 the other hand, mothers breeding in poor body condition or an unfavorable environment might
57 overproduce the sex that is less costly to rear, thereby facilitating their own survival and thus
58 future breeding probability (Gomendio et al. 1990). Notably, the less sensitive and the less
59 expensive sex may often be the same, making these hypotheses difficult to distinguish.

60 To date, parental morphological traits (i.e. body condition and body size), male
61 secondary sexual characters (i.e. plumage and song features) and ecological factors (usually
62 some indicator of food availability) have been considered as cues for brood sex ratio
63 adjustment, while behavioral traits of the partner have been ignored. Recent results on
64 behavioral traits, however, suggest that these could be as important determinants in brood sex
65 ratio adjustment as morphological traits. First, behavioral traits show consistent variation
66 across time and contexts even among individuals of the same sex and age (Réale et al. 2007;
67 Bell et al. 2009). Second, selection experiments have demonstrated that this variation has a
68 partly genetic background (van Oers et al. 2005; Fidler et al. 2007). Third, behavioral traits
69 may have different impact on male and female fitness (Dingemanse et al. 2004; Dunn et al.
70 2011). Therefore, we can expect that the behavior of parents influences the fate of the
71 offspring in a sex-specific way via either genetic inheritance or parental care.

72 To test the hypothesis that the behavior of the partner plays a role in brood sex ratio
73 adjustment, we performed an exploratory study on the relationship between male aggression
74 and offspring sex ratio in a wild population of a small passerine, the collared flycatcher
75 (*Ficedula albicollis*). Aggression is one of the most important and most widely studied
76 behavioral traits, owing to its close link to fitness. In collared flycatcher males, aggression is
77 repeatable in a single context and correlated across multiple contexts, indicating individual
78 personalities (Garamszegi et al. 2006; Garamszegi et al. 2012). Moreover, aggression may
79 give comprehensive information about the behavior of the males because functionally
80 different behavioral traits (e.g. aggression and exploration) correlate with each other within an
81 individual and form a behavioral syndrome (Garamszegi et al. 2009).

82 Male aggression is likely to be involved in brood sex ratio adjustment because females
83 can assess it before egg laying in at least two different ways. First, more aggressive males
84 may court more intensively, because intra- and inter-sexual behaviors are governed by a

85 shared physiological background (Eising et al. 2006). Additionally, more aggressive males
86 may also act more violently when courting, for example force females to copulate or cause
87 physical injury to them (Ophir and Galef 2003). Second, females can gain information about
88 male aggression directly by eavesdropping on male-male interactions before pairing (Naguib
89 and Todd 1997; Otter et al. 1999).

90 Male aggression may have sex-specific impact on offspring fitness via genetic
91 inheritance because aggression has a moderate heritability (e.g. in the house mouse (*Mus*
92 *musculus domesticus*), $h^2=0.30$ in van Oortmerssen and Bakker 1981 and $h^2=0.40$ in Gammie
93 et al. 2006; in the western bluebird (*Sialia mexicana*), $h^2=0.45$ in Duckworth and Badyaev
94 2007) and male reproductive success may be more dependent on aggression than female
95 reproductive success. In the collared flycatcher, aggression is necessary for males to
96 successfully compete with each other for breeding territories and thus attract mates. Male
97 aggression may have sex-specific impact on offspring fitness also via parental care, because
98 mating and parental behaviors are often conflicting (Ketterson et al. 1992; Stoehr and Hill
99 2000; Peters 2002) and the future prospects of male and female offspring may be differently
100 dependent on parental investment. In our study population, male offspring have greater
101 growth potential but are also more sensitive, so under good conditions male, while under poor
102 conditions female offspring perform better (Rosivall et al. 2010; Hegyi et al. 2011).
103 Altogether, we predicted one of two scenarios for male aggression related brood sex ratio
104 adjustment. First, if aggression is particularly advantageous for males in terms of reproductive
105 success, mates of more aggressive males might overproduce sons, while mates of less
106 aggressive males might overproduce daughters. Second, if aggression in males is negatively
107 related to their contribution to parental care, mates of more aggressive males might
108 overproduce daughters, while mates of less aggressive males might overproduce sons.

109

110 **Methods**

111 Data collection

112 The study was conducted in a nest box breeding population of the collared flycatcher, in the
113 Pilis Mountains, Hungary (47°43'N, 19°01'E). The collared flycatcher is an insectivorous,
114 migratory, secondary hole-breeding, primarily monogamous passerine with normally one
115 clutch per breeding season. The most common clutch size is 6-7 eggs. Only females incubate
116 the eggs, but both parents care for the nestlings. Males arrive at the breeding site before
117 females and immediately start to acquire and defend nest boxes. They then begin to attract
118 arriving females by singing, displaying and presenting their nest box (Cramp and Perrins
119 1993).

120 We measured male aggression at this courtship stage (in the middle of April) by
121 presenting territory owner males with a live decoy male to stimulate male-male aggression.
122 Stimulus males were placed in a small wire cage (20x15x15 cm), so the focal males were not
123 able to injure them. Multiple stimulus males were randomly used across tests and were
124 unfamiliar with the owner males. Tests were made during the most active period (between
125 5:00 a.m. and 10:00 a.m.) and under good weather conditions. To quantify aggression, we
126 recorded the latency of the first attack of the focal male, which was the time elapsed between
127 the detection of and the first attack toward the intruder male. The detection was defined as the
128 appearance of the owner male on its territory, and the first attack as the first event when the
129 owner male touched the cage of the intruder male (usually with clear intention to fight). The
130 latency of the first attack is a reliable measure of aggression, since it is repeatable within
131 males ($R=0.383$ in Garamszegi et al. 2012) and correlates with other variables describing
132 territorial aggression (e.g. frequency and average duration of attacks, see Garamszegi et al.
133 2006). The tests lasted five minutes (after the appearance of the focal male), because
134 according to our previous observations, males that did not respond to the stimulus in terms of

135 aggressive approach within five minutes did not respond at all. As previously, non-responder
136 focal males were given a score of 301 sec for attack latency (Garamszegi et al. 2006).

137 After the behavioral test, focal males were trapped for ringing and morphological
138 measurements. We measured the size of two white plumage characters of the males, the
139 forehead patch and the wing patch, which are important in social interactions (Garamszegi et
140 al. 2006; Hegyi et al. 2010), and tarsus length as an indicator of structural body size. Based on
141 the color of the remiges, males were categorized as yearlings or adults (Svensson 1992).
142 Following the measurements, males were released and their breeding attempt was monitored
143 to assess the date of the first egg and the total number of eggs laid by their mates. To
144 determine brood sex ratio, we collected small blood samples from the nestlings (at the age of
145 9-13 days) and embryonic tissue samples from the unhatched fertile eggs. The protocol of the
146 molecular sex determination had been validated on adults of known sex, for details see
147 Rosivall et al. (2004). In total, out of the 171 eggs laid in 27 broods, 150 were sexed from
148 nestling blood sample, 5 from embryonic tissue sample and 2 were unfertile. We had no
149 information about 4 eggs and 10 nestlings that had disappeared before sampling. Therefore,
150 we had complete information on the sex ratio for 17 broods, while incomplete information
151 was available for an additional 10 broods that were also used in the analysis.

152

153 Data analysis

154 The analysis included 27 broods (from 27 different pairs) from three years (6 broods from
155 2005, 14 broods from 2007 and 7 broods from 2010). We analyzed the data by fitting a
156 generalized linear mixed model with binomial error distribution, logit link function and
157 Satterthwaite's approximation of degrees of freedom. We used the number of male offspring
158 in the brood as the dependent variable and the total number of sexed offspring as the binomial
159 denominator, so brood sex ratio refers to the proportion of male offspring in the brood. The

160 fixed variables entered in the initial model were the latency of the first attack (logarithmically
161 transformed), the wing patch size (standardized across age categories; see Török et al. 2003),
162 the tarsus length and the binary age of the male, the laying date of the first egg (as a deviation
163 from the median clutch initiation date of the given year) and year. The explanatory variables
164 were statistically independent of each other (all $p > 0.1$). To account for the possible
165 confounding effect of the stimulus male (Garamszegi et al. 2006), the identity of the stimulus
166 male was also included in our model as a random factor. Non-significant variables were
167 removed one by one using a backward stepwise selection procedure. We present F -statistic
168 values for each explanatory variable and effect size (Pearson's r) with 95% confidence
169 intervals calculated from F -values according to Rosenthal (1994). The analysis was
170 performed in SAS version 9.1 using the GLIMMIX macro (SAS Institute Inc., USA, 1990).
171 Neither embryo nor nestling mortality is sex-biased in our study population (our unpublished
172 results). Moreover, the proportion of sampled progenies in the brood was independent of all
173 the explanatory variables considered in the analyses of brood sex ratios (all $p > 0.1$). Therefore,
174 the analyzed brood sex ratios can be regarded as primary brood sex ratios (i.e. sex ratios at
175 egg laying).

176

177 **Results**

178 We found a significant positive relationship between the sex ratio of the brood and the latency
179 of the first attack of the male (Fig. 1, Table 1). Given that there is an inverse relationship
180 between attack latency and aggression (i.e. the more aggressive the male, the faster he
181 attacks), the direction of the relationship indicates that the proportion of sons in the brood
182 decreased with the aggression of the father. The brood sex ratio was significantly positively
183 related to the tarsus length of the male (Fig. 2, Table 1) and significantly declined with the
184 progress of the breeding season (Table 1). There was a non-significant tendency for an

185 increase in brood sex ratio with male wing patch size, but brood sex ratio was not affected by
186 male forehead patch size, male age and year (Table 1).

187

188 **Discussion**

189 Manipulating the sex ratio of the brood may be adaptive, whenever the fitness of male and
190 female offspring is differentially influenced by parental attributes or environmental factors.
191 The behavior of parents is likely to influence the fitness of male and female offspring
192 differently for at least two reasons. First, behavioral traits may be at least partially heritable
193 (van Oers et al. 2005) and the sexes may have different fitness optima for shared behavioral
194 traits (Dingemanse et al. 2004; Dunn et al. 2011). Second, there may be an association
195 between parental behavior and the quality of care (e.g. Both et al. 2005; Duckworth 2006) and
196 the sexes are known to differ in their early susceptibility to rearing conditions in many species
197 (Råberg et al. 2005).

198 Our study is the first that regards a behavioral trait of the partner as a possible predictor
199 of brood sex ratio in animals. We demonstrated in a wild bird population that aggressive
200 behavior of the male during the period of mate attraction is related to the proportion of sons in
201 his subsequent brood. The less aggression was displayed by the male in a simulated territorial
202 conflict, the more sons were produced by his mate.

203 This relationship can be adaptive, if more aggressive males contribute less to parental
204 care and female offspring are less sensitive to rearing conditions. Actually, in the same
205 collared flycatcher population, male nestlings grew faster in experimentally reduced broods,
206 but grew slower in experimentally enlarged broods than female nestlings (Rosivall et al.
207 2010). Furthermore, food supply, estimated by caterpillar abundance, had a stronger effect on
208 body mass growth in male than in female nestlings (Hegyi et al. 2011). This suggests that
209 males have a greater growth potential but are more sensitive, thus profiting more from

210 favorable rearing conditions and suffering more from unfavorable rearing conditions than
211 females. Although we have no direct data linking male aggression to parental care, assuming
212 such a link is reasonable in birds. In males, testosterone has a conflicting effect on mating and
213 parental effort, as it facilitates sexual and aggressive behaviors, while suppresses parental
214 behaviors (Wingfield et al. 1987). Furthermore, the magnitude and duration of testosterone
215 elevation during the breeding season has been reported to vary among males and suggested to
216 be the basis for some of the individual variation in allocation to mating versus parental effort
217 (reviewed by Kempenaers et al. 2008). In the pied flycatcher (*Ficedula hypoleuca*), the
218 sibling species of our study species, testosterone treated males prolonged their singing activity
219 and acquired more territories, while, at a later phase, they performed negligible feeding
220 activity or abandoned their brood (Silverin 1980). In the western bluebird, males that were
221 more aggressive towards conspecific males in a simulated territorial conflict fed their
222 nestlings at a lower rate (Duckworth 2006). Additionally, there is indication in both pied and
223 collared flycatchers, that reduced paternal contribution to nestling feeding reduces the
224 fledging success of the brood (Silverin 1980; Garamszegi et al. 2004). Consequently, if a
225 trade-off between allocation to male aggression and nestling care exists in our collared
226 flycatcher population, mates of more aggressive males may maximize their fitness benefit by
227 producing disproportionately more daughters, because these nestlings may suffer less from
228 the reduced paternal provision and thus fledge with higher success. Mothers receiving less
229 help from their mate can also enhance their own survival through such an adjustment because
230 female nestlings may impose less cost on them due to their smaller energy demand. Producing
231 disproportionately more sons when mated to a less aggressive male may be beneficial for
232 mothers because male nestlings may perform better in case of intensive male assistance in
233 parental care. In addition, the fitness benefit through good-provisioned sons may exceed the
234 fitness benefit through good-provisioned daughters in our population, due to a greater

235 reproductive potential for males created by polygynous mating and extra-pair fertilizations
236 (Garamszegi et al. 2004; Rosivall et al. 2009).

237 The results contradict our alternative scenario of a positive relationship between brood
238 sex ratio and paternal aggression, which would require that the heritable variation in
239 aggression is linked to reproductive success in a sex-dependent way. Perhaps a sex-difference
240 in developmental sensitivity or early energy requirement provokes stronger selection for
241 brood sex ratio adjustment to paternal aggression in the opposite direction because it not only
242 influences the number of offspring produced, but also the chance whether or not an individual
243 reaches reproductive age. Furthermore, the benefits of inherited aggression may not be limited
244 to males, as female collared flycatchers also perform aggression towards same-sex intruders,
245 which may help them to prevent polygynous mating (Garamszegi et al. 2004; Hegyi et al.
246 2008).

247 As in a previous study (Rosivall et al. 2004), the clutch initiation date had a significant
248 effect on the brood sex ratio. However, because the territorial intrusion tests were conducted
249 in a relatively short period due to logistic constraints, the clutch initiation dates in the present
250 study do not characterize the entire population. Therefore, this result has to be handled
251 carefully. Nonetheless, the negative relationship between brood sex ratio and laying date may
252 partially be driven by selective pressures similar to those suggested for the negative
253 relationship between brood sex ratio and male aggression. Namely, if early in the season food
254 is more abundant, mothers might maximize their fitness benefit by producing an excess of
255 sons, which may perform better than daughters under favorable conditions. As food becomes
256 scarcer with the progress of the season and mothers also face energetic constraints due to the
257 upcoming molt and migration, they might maximize their fitness benefit by producing an
258 excess of daughters, the sex that performs better under unfavorable conditions and requires
259 less expenditure to rear. For a better understanding of the seasonal brood sex ratio pattern in

260 our study population, a more detailed analysis of the temporal distribution of food is needed,
261 as food abundance and brood sex ratio may not simply decrease during the breeding season
262 but may show more complex patterns. For example, our previous study focusing on a single
263 year when birds arrived at the breeding site in two distinct waves, found an increase in brood
264 sex ratio for the whole season (Rosivall et al. 2004), no shift for the first wave separately and
265 a decrease for the second wave separately (our unpublished results). Still, timing of breeding
266 seems to be an important factor in sex ratio adjustment of collared flycatcher females, at least
267 in the central area of the species, as in a Czech population, Bowers et al. (2013) also found
268 indication for a seasonal decrease in brood sex ratio.

269 Contrary to the results in a Swedish population (Ellegren et al. 1996) and in line with
270 our previous report (Rosivall et al. 2004), we did not find significant relationship between
271 male forehead patch size and brood sex ratio. There was, however, a non-significant tendency
272 for a positive relationship between the wing patch size of the male and the proportion of sons
273 in the brood. Such relationship was not found previously (Rosivall et al. 2004). It is plausible
274 that the benefit of sex ratio adjustment in relation to male attractiveness is context-dependent,
275 because other selective pressures, such as year quality, that act on offspring survival rather
276 than future reproductive success may override its importance (see e.g. Addison et al. 2008).
277 The between-population difference in the role of male ornaments can be explained by the
278 different information content of these traits. In our study population, wing patch size is
279 condition-dependent (Török et al. 2003) and has both intra- and intersexual function
280 (Garamszegi et al. 2006; Hegyi et al. 2010), while in the Swedish population, forehead patch
281 size serves as a condition-dependent quality indicator (Gustafsson et al. 1995). The results in
282 the Czech population were similar to ours, that is brood sex ratio was positively related to
283 male wing patch size and unrelated to male forehead patch size (Bowers et al. 2013).
284 According to some recent theoretical work (Booksmythe et al. 2013), the difference among

285 populations in sex ratio adjustment in relation to male ornamentation may reflect population
286 difference in the coupled evolution of male ornament expression level, female preference and
287 facultative sex allocation.

288 We found that male tarsus length was a significant predictor of brood sex ratio. Note
289 that the effect of paternal body size on brood sex ratio was independent of the effect of
290 paternal aggression, since the two male characteristics were unrelated. Though, in our
291 previous study, the provisioning activity of parents was not linked to their own or their mate's
292 tarsus length (Kiss et al. 2013), if larger body size is associated with access to superior
293 territories, as in the Swedish population (Gustafsson 1988), the positive relationship between
294 brood sex ratio and paternal tarsus length could also be explained by the sex-specific response
295 of nestlings to rearing conditions (Rosivall et al. 2010; Hegyi et al. 2011). Unfortunately, in
296 the Czech population, male tarsus length was not considered (Bowers et al. 2013), however,
297 interestingly, in the Swedish population, male tarsus length did not affect brood sex ratio
298 (Ellegren et al. 1996).

299 To conclude, our results provide evidence for the so far untested hypothesis that,
300 considering their potential sex-specific effects on offspring fitness, behavioral traits of the
301 partner can be involved in brood sex ratio adjustment. We believe that extending the analyses
302 on brood sex ratio adjustment to the behavior of the partner may help explain some apparent
303 discrepancies in the literature. For example, regarding the general negative link between
304 mating and parental effort mediated by a shared hormonal background, selection for offspring
305 sex ratio adjustment to the level of male care can account for the lack of an expected
306 relationship between offspring sex ratio and male sexual ornaments, that is, attractiveness.
307 Further studies in multiple systems are clearly needed to test the generality of the
308 phenomenon we described here.

309 **Acknowledgements**

310 We thank Rita Föző, Márton Herényi, Dorottya Kiss, Miklós Laczi, Gergely Nagy and Sándor
311 Zsebők for their help in the field and the lab and two anonymous referees for their valuable
312 comments on the manuscript. We are also very grateful to the Pilis Park Forestry for its
313 support.

314

315 **Funding**

316 The study was supported by grants from the Hungarian Scientific Research Found (grant no.
317 F68295, PD75481, K75618, K101611), the Social Renewal Operational Programme of the
318 Hungarian Government (TÁMOP 4.2.1./B-09/1-KMR-2010-0005 and 4.2.2./B-10/1-2010-
319 0023), the Hungarian State PhD Scholarship to E. Szász, the Erdők a Közjóért Alapítvány,
320 and the “Plan Nacional” program of the Spanish Government (ref. no. CGL2009-10652).

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448 **Figure captions**

449 **Fig. 1**

450 Brood sex ratio in relation to paternal attack latency in the collared flycatcher. Given that
451 there is an inverse relationship between attack latency and aggression (i.e. the more
452 aggressive the male, the faster he attacks), the direction of the relationship indicates that the
453 proportion of sons in the brood decreased with the aggression of the father

454

455 **Fig. 2**

456 Brood sex ratio in relation to paternal tarsus length in the collared flycatcher

457 **Table 1**

458 Brood sex ratio in relation to paternal phenotype, laying date and year, in the collared
 459 flycatcher

Variable	<i>df</i>	<i>F</i>	<i>p</i>	<i>r</i>	95% CI
Attack latency	1, 23.00	10.78	0.003	0.565	0.235–0.778
Tarsus length	1, 9.19	11.20	0.008	0.741	0.503–0.875
Laying date	1, 10.50	9.10	0.012	0.681	0.407–0.843
Wing patch size	1, 6.45	4.18	0.084	0.627	0.324–0.813
Forehead patch size	1, 15.20	0.39	0.540	0.158	-0.236–0.508
Age	1, 8.23	0.81	0.393	0.299	-0.091–0.610
Year	2, 6.00	0.07	0.934	0.151	-0.243–0.502

460

461 Generalized linear mixed model with binomial error, logit link and Satterthwaite's
 462 approximation of degrees of freedom. Variables retained in the final model are indicated in
 463 bold. Values for non-significant variables are derived from models where these variables were
 464 reintroduced to the final model one by one