RESEARCH ARTICLE

Are brood sex ratios adaptive?—The effect of experimentally altered brood sex ratio on nestling growth, mortality and recruitment

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Abstract

Brood sex ratios (BSRs) have often been found to be nonrandom in respect of parental and environmental quality, and many hypotheses suggest that nonrandom sex ratios can be adaptive. To specifically test the adaptive value of biased BSRs, it is crucial to disentangle the consequences of BSR and maternal effects. In multiparous species, this requires cross-fostering experiments where foster parents rear offspring originating from multiple broods, and where the interactive effect of original and manipulated BSR on fitness components is tested. To our knowledge, our study on collared flycatchers (*Ficedula albicollis*) is the first that meets these requirements. In this species, where BSRs had previously been shown to be related to parental characteristics, we altered the original BSR of the parents shortly after hatching by cross-fostering nestlings among trios of broods and examined the effects on growth, mortality and recruitment of the nestlings. We found that original and experimental BSR, as well as the interaction of the two, were unrelated to the fitness components considered. Nestling growth was related only to background variables, namely brood size and hatching rank. Nestling mortality was related only to hatching asynchrony. Our results therefore do not support that the observed BSRs are adaptive in our study population. However, we cannot exclude the possibility of direct effects of experimentally altered BSRs on parental fitness, which should be evaluated in the future. In addition, studies similar to ours are required on various species to get a clearer picture of the adaptive value of nonrandom BSRs.

KEYWORDS
adaptivity, cross-fostering, fitness, nestling development, rearing conditions, recapture probability, sex allocation, sex ratio adjustment

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1 | INTRODUCTION

Sex of the offspring can be an important determinant of fitness, as survival and future reproductive success of male and female offspring can be shaped differently by selective forces. When the average fitness returns through male and female offspring differ and can be predicted by parental or environmental quality, conditional production of male and female offspring is expected to evolve (Trivers & Willard, 1973). As follows, within families, we expect deviations from the even offspring sex ratio towards the sex that has the higher fitness potential given the quality of the parents and the environment. In this way, within families, offspring of the sex produced in surplus should contribute to parental fitness more than offspring of the other sex, and the fitness return of the parents should be maximized. In vertebrates with chromosomal sex determination, such as birds and mammals, including humans, the primary offspring sex ratio was found to be correlated, for example, with body condition, mating status, social rank and sexual attractiveness of the parents and food availability during reproduction (for reviews see: Cockburn et al., 2002; Lazarus, 2002; Szász et al., 2012). However, multiple studies failed to find support for these relationships or found differences between study years or populations (see the reviews), therefore multiple meta-analyses were performed on sex ratio adjustment. These substantially differed in their approach. Some (Booksmythe et al., 2017; Cassey et al., 2006) took into account all predictors equally (i.e. not only those that had been proved to have sex-specific roles or fitness consequences). These found only partial (Cassey et al., 2006) or not convincing (Booksmythe et al., 2017) support for sex ratio adjustment. Some other meta-analyses took into account only those predictors that had been proved to be relevant to sex ratio adjustment or included all predictors but specifically took into account their relevance to sex ratio adjustment (Cameron, 2004; Sheldon & West, 2004; Szász et al., 2019; West & Sheldon, 2002). These meta-analyses consistently found overall support for sex ratio adjustment, and where it was specifically tested, the effect sizes for relevant traits were significantly larger than for traits with unknown relevance (Cameron, 2004; Szász et al., 2019).

To prove that sex ratio adjustment is an existing phenomenon, experimental studies that manipulated certain parental and environmental characteristics have been performed. Such experiments led to heterogeneous results (Bradbury & Blakey, 1998; Delhey et al., 2007; Ellegren et al., 1996; Kilner, 1998; Korsten et al., 2006; Rutstein et al., 2004; Saino et al., 1999; Sheldon et al., 1999). Though these kinds of experimental studies are certainly important to confirm or reject the relationships that were found in correlative studies between parental/environmental characteristics and offspring sex ratio, they still do not provide insight into the adaptive value of offspring sex ratio patterns. So far, mainly a few correlative studies have investigated the fitness consequences of biased offspring sex ratios. For example, the brood sex ratio of the offspring was found to be correlated with parental colouration (barn owl [*Tyto alba*]; Roulin et al., 2010) or natal territory quality (tawny owl [*Strix aluco*]; Appleby et al., 1997) in a way that offspring of the sex with

better survival or reproductive chances have been overproduced. In the red deer (*Cervus elaphus*), dominant mothers were more likely to produce male offspring than subordinate mothers (Clutton-Brock et al., 1984, 1986), and this pattern was suggested to be evolutionary advantageous from the point of future reproductive success of the offspring (Clutton-Brock et al., 1984, 1986) and residual reproductive success of the mother (Gomendio et al., 1990). However, a later study (Kruuk et al., 1999) found the relationship between maternal dominance status and calf sex to be year-dependent, probably because the higher mortality of male calves under poor condition cancels the benefits of such a pattern. Regarding humans, multiple studies that had investigated entirely different populations (Roma populations in Hungary, US billionaires and a rural Chinese population; Bereczkei & Dunbar, 1997; Cameron & Dalerum, 2009; Luo et al., 2017, respectively) found that parents produced more children of the sex through which they had more grandchildren. Altogether, these correlative studies consistently found that the parents produced offspring sex ratios biased towards the sex that provided the higher fitness return under the prevailing circumstances, suggesting that sex ratio adjustment is adaptive. However, to confirm the causal link between offspring sex ratio and the fitness return of the parents, it is important to experimentally decouple offspring sex ratio from the parental genetic background and early maternal effects by cross-fostering (see later).

Several cross-fostering studies have already manipulated the sex ratio of the offspring with various purposes, such as studying sibling competition (Nicolaus et al., 2009; Radersma et al., 2011), investigating the relationship between the rearing capability of the parents and their original brood sex ratio (Bowers et al., 2013) or revealing the rearing costs of male and female offspring (Koskela et al., 2009; Rutkowska et al., 2011). However, to specifically assess whether brood sex ratios are adaptive, we should study the fitness return not only in relation to the experimentally manipulated offspring sex ratio but also to the interaction between the experimentally manipulated and the original offspring sex ratio of the foster parents. Namely, if parents are selected to maximize their fitness by producing an individually optimal ratio of male and female offspring, the fitness costs of rearing a male- or female-biased brood may be dependent on whether the parents originally produced a male- or female-biased offspring sex ratio. To our knowledge, the interactive effect of original and experimental sex ratio has so far been tested only in captive tammar wallabies (*Macropus eugenii derbianus*; Robert et al., 2010; Schwanz & Robert, 2016). These studies found that foster offspring reared by mothers that originally produced a male offspring were more likely to survive until weaning, but the sex of the foster offspring and its interaction with the sex of the original offspring had no effect on weaning success, and the body mass of the foster offspring at weaning and one year of age (Robert et al., 2010). However, mothers that weaned the sex opposite of what they originally produced were less likely to give birth in the following year (Schwanz & Robert, 2016). Thus this study provided experimental evidence that parents produced the sex that yielded higher fitness return.

The present experimental study was designed specifically to investigate the parental fitness return in relation to offspring sex ratio using a multiparous avian model species, the collared flycatcher. This species is an excellent object for such a study because nonrandom sex ratios have been reported in multiple populations (Bowers et al., 2013; Ellegren et al., 1996; Rosivall et al., 2004; Szász et al., 2014) and it is likely that the average fitness return through male and female offspring differ between parents of different individual/environmental quality for at least two reasons. First, in our study population, male offspring were shown to be more sensitive to early environmental conditions, as under favourable rearing conditions (experimentally reduced brood size) they were capable to grow faster than female offspring, but under unfavourable rearing conditions (experimentally enlarged brood size), they lagged behind (Rosivall et al., 2010). Additionally, year quality had a stronger effect on the growth rate of male nestlings than that of female nestlings (Hegyi et al., 2011). These results suggest that male offspring have a higher energy requirement and as a consequence, may be more costly to rear. Second, the reproductive success of male collared flycatchers is likely to be more variable than that of females due to occasional polygyny and frequent extra-pair copulations. In our study population, at least 5% of the males is polygynous (Garamszegi et al., 2004; Herényi et al., 2012), and extra-pair offspring can be found in 56% of the broods, and 21% of the offspring is sired by extra-pair male (Rosivall et al., 2009). As follows, the future reproductive success of male offspring is expected to be more dependent on parental care than that of female offspring, which is supported by our previous results, as early environmental conditions (brood size manipulation) had a significant effect on lifetime reproductive success exclusively in males (Szász et al., 2017).

To assess the adaptive value of brood sex ratio adjustment, we experimentally altered the brood sex ratio of collared flycatchers by cross-fostering nestlings shortly after hatching so that the parents reared broods of random sex ratio after the manipulation. First, we expected a positive relationship between the development and survival of the offspring and the original brood sex ratio of the foster parents assuming that better quality parents, perhaps also having a better territory, have a male-biased offspring sex ratio and provide better parental care. Second, because those foster parents that rear a surplus of males are likely to be more challenged, we expected a negative relationship between the development and survival of the offspring and the experimental brood sex ratio of the foster parents. Third, as the rearing costs of males are supposedly unequal for parents of different qualities, we expected an interactive effect of the experimental brood sex ratio and the original brood sex ratio of the foster parents on the development and survival of the offspring. Specifically, if sex ratio adjustment is adaptive, parents that originally produced male-biased broods (and are assumed to be of better quality and have higher caregiving capability) are expected to raise male-biased foster broods more successfully than parents that originally produced female-biased broods.

2 | MATERIALS AND METHODS

2.1 | Study site and study species

Data were collected in a nest-box breeding population of the collared flycatcher in the Pilis-Visegrádi Mountains, Hungary (47°43′N, 19°01′E). The study site is situated in a protected, middle-aged, oak-dominated forest.

The collared flycatcher is a small (ca. 13 g), migratory, insectivorous, primarily socially monogamous, hole-nesting passerine that breeds in deciduous forests in Europe and prefers artificial nest boxes over natural cavities (Lundberg et al., 1981; Mitrus, 2003). Collared flycatcher females lay one clutch per breeding season (except for replacement clutches) containing typically 5–7 eggs that hatch ca. 12 days after clutch completion. Because females start to incubate prior to clutch completion, there is an age difference between the first and the last hatched nestling that ranges between half-day and 2 days (Rosivall et al., 2005). Nestlings remain in the nest for ca. 14–15 days after hatching, while being fed by both parents. Natal dispersal of collared flycatchers is suggested to be low (Pärt, 1990), and the majority of the recruits start to breed in their first or second year after fledging (Herényi et al., 2012; Szász et al., 2017; our unpublished results).

2.2 | Field procedures

The study was conducted in two consecutive breeding seasons (2017–2018). At the beginning of the breeding season, we regularly visited our nest boxes for newly initiated clutches. Around the expected hatching dates, the nest boxes were visited daily to register the exact age and number of the hatched nestlings. We experimentally altered the original brood sex ratio on day 2 posthatch (day 0 = hatching date). We randomly swapped nestlings among trios of broods (15 and 10 trios in 2017 and 2018, respectively) that hatched on the same day and were of similar size (the maximum difference in brood size within trios was one nestling and in most cases, the three broods were of the same size). As a result of the cross-fostering, all foster parents involved in our analyses reared the same number of nestlings as they hatched and all nestlings were unrelated to the foster parents with an approximately equal proportion of nestlings from the other two broods of the experimental trio (Figure 1). During swapping, we transported the nestlings in soft cotton bags placed in boxes heated with reusable pocket warmer packs. Once we created the foster brood, we measured the body mass of each nestling with Pesola spring balance (to the nearest 0.1 g) and marked them individually by removing tufts from their head and back. We measured the body mass of the nestlings every second day until day 14 posthatch. On day 6 posthatch, we ringed the nestlings with individually numbered, coloured aluminium rings. On day 8 posthatch, we took a drop of blood from the wing vein of each nestling for the purpose of molecular sex determination. On day 9 posthatch, we caught the parents with conventional spring traps for identification and morphological measurements. Nestling

mortalities were noted and from all nestlings that died before blood sampling, we preserved a small tissue sample for molecular sex determination. All eggs that were still unhatched on day 2 posthatch were candled. As none of them contained living embryos, they were collected and inspected for signs of embryonic development and when it was applicable, we preserved embryonic tissue samples for molecular sex determination. Nestling recruitment from the foster broods was assessed by systematic searching for the colour-ringed birds in every study year following the experiment (2018–2021). We caught the recruited birds with spring traps during the courtship or the nestling feeding period for individual identification.

As male and female collared flycatcher nestlings are monomorphic in size and plumage, the cross-fostering was blind to the sex of the nestlings. After the field season, we performed the molecular sex

determinations using the F2550 and the R2718 primers (Fridolfsson & Ellegren, 1999) and the protocol described in Rosivall et al. (2004). Then, we calculated the original primary brood sex ratios, including the sex of the dead nestlings and unhatched eggs, and the experimental brood sex ratios resulted from the cross-fostering. We found that we successfully altered the original brood sex ratios and as a result, a fraction of the foster parents reared either a more or less male-biased brood compared with their original brood sex ratio, while some reared a brood with a sex ratio similar to their original brood. The change in the number of male nestlings in the brood after the cross-fostering ranged between −4 and +4 and its distribution was symmetric (Figure 2a). The experimental brood sex ratio resulted from the cross-fostering was statistically independent of the original brood sex ratio ($r = -0.094$; Figure 2b).
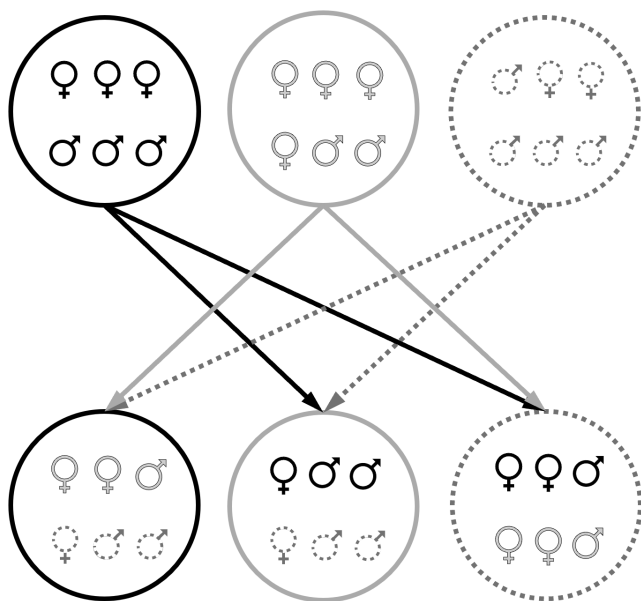
2.3 | Statistical analysis

2.3.1 | Nestling development

We analysed the relationship between experimentally altered brood sex ratio and nestling development in R statistical environment (version 4.1.3; R Core Team, 2022) building a general linear mixed model (GLMM) with Gaussian error distribution (using the function 'lmer' of the package 'lme4' [Bates et al., 2015]) and 'contr.sum' setting. From the analysis, we omitted those broods that were reared by only one parent, were secondary broods of polygynous males, where the original or experimental brood sex ratio was unknown due to the disappearance of nestlings (probably due to depredation), where a nestling died between the manipulation (day 2 posthatch) and the end of the intense growth period (day 10 posthatch) resulting in changes in two explanatory variables: brood size and experimental brood sex ratio, and a brood not measured for logistic reasons. Altogether, we included 339 nestlings from 54 broods (32 and 22 broods with 199 and 140 nestlings in 2017 and 2018, respectively) in the statistical analysis.

Nestling body mass generally changes along a sigmoid curve; however, in case of some late hatched nestlings (especially under poor food conditions), the curve is closer to the linear shape resulting in the erroneous estimation of the logistic growth constant (Rosivall et al., 2010). Therefore, similarly to the earlier study of Rosivall et al. (2010), instead of using the logistic growth constant, we rather
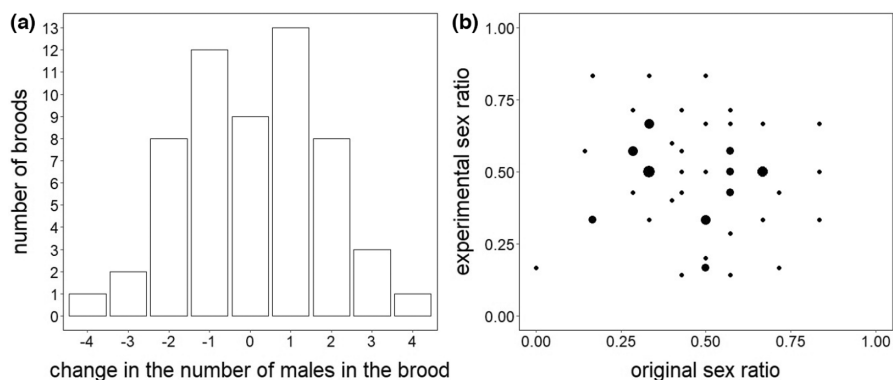

FIGURE 1 The design of our experimental brood sex ratio manipulation. The circles represent the broods and the male/female symbols represent the nestlings. The upper part depicts the experimental brood trio before the cross-fostering and the lower part after the cross-fostering. The broods were chosen randomly with respect to brood sex ratio, and the nestlings were cross-fostered randomly with respect to sex, so the original and the experimental brood sex ratios differed among trios.

FIGURE 2 (a) The change in the number of male nestlings in collared flycatcher broods as a result of our experimental brood sex ratio manipulation. (b) The statistical independence of the original and the experimental brood sex ratios. $N = 57$ broods (dot sizes indicate the number of samples from 1 to 5).

used the maximum body mass gain of the nestlings to describe nestling development. To do so, we calculated the average hourly body mass gain of the nestlings between day 4–8 and day 6–10 posthatch (i.e. during the most intense, quasi-linear growth period) by dividing the body mass gain by the number of active hours between the measurements on days 4 and 8, or days 6 and 10, respectively. The number of active hours was the time passed between the two measurements minus the inactive evening hours (8 hours a day according to Müller, 1993). To get the maximum body mass gain, we selected the larger of the two body mass gain values. In the statistical analysis, the response variable was the squared maximum body mass gain to ensure the normal distribution of the model residuals.

The explanatory variables were the original brood sex ratio, the experimental brood sex ratio and the interaction of these two variables. In the initial model, we also included the sex and the relative 2-day body mass of the nestlings. The body mass on day 2 posthatch relative to brood average is a good proxy of hatching rank (Rosivall et al., 2005). We also introduced the brood size as a categorical variable distinguishing smaller broods with 5–6 nestlings (these broods were combined in one group because we had only 3 broods with 5 nestlings) and larger broods with 7 nestlings, year and the interaction of year with all variables, including the three-way interaction of experimental brood sex ratio and original brood sex ratio and year. When a year interaction turned out to be significant, we run post hoc GLMMs for the two study years separately. To control for the nonindependence of nestlings due to shared genetic, maternal and environmental effects, we introduced the original brood ID and the foster brood ID of the nestlings as random factors. Multicollinearity among the explanatory variables was not an issue, as Variance Inflation Factor (VIF) values for the initial model (not containing the interactive terms) were sufficiently small (all VIF <1.081; using function 'vif' from R package 'car' [Fox & Weisberg, 2019]). Fit of the initial model was validated visually by plotting the model residuals against the predicted values of the model (using function 'plot' from R package 'graphics' [R Core Team, 2022]).

We applied backward-stepwise elimination of nonsignificant terms ($p > 0.05$) to find the model best explaining the variation in nestling development. Then, we have added the removed explanatory variables to the final model one by one (in the case of interactive terms, with the constituent main effects) to obtain reliable parameter estimates (Hegyi & Laczi, 2015). We present Type III F tests with Satterthwaite's approximation of degrees of freedom (using function 'anova' from package 'lmerTest' [Kuznetsova et al., 2017]). We tested the significance of the random factors with Log Likelihood Ratio Tests.

2.3.2 | Nestling mortality and recruitment

We analysed the relationship between experimentally altered brood sex ratio and the occurrence of nestling mortality/rate of nestling recruitment at the brood level building a generalized linear model with binomial error distribution and logit link function (using the function 'glm' of the R package 'stats' [R Core Team, 2022]). From the analysis, we omitted those broods that were not cared by two parents

throughout or in part of the nestling stage, broods that were secondary broods of polygynous males, and broods where nestling(s) died due to external injury or disappeared probably due to depredation, or where the original or experimental brood sex ratio was unknown due to the disappearance of nestlings, or where a nestling died within a day after the start of cross-fostering (resulting in reduced brood size not caused by the treatment) and a brood not measured for logistic reasons. The sample size was 57 broods in these analyses (33 and 24 broods in 2017 and 2018, respectively).

In the analysis of nestling mortality, the binary response variable was whether all nestlings reached fledging age or at least one nestling died in the foster brood during nestling development between day 2 and day 14 posthatch. In the analysis of nestling recruitment, we used the number of nestlings recaptured from the foster brood as the response variable and the original number of nestlings in that brood as the binomial denominator. The explanatory variables were the original brood sex ratio, the experimental brood sex ratio and the interaction of these two variables. In the initial model, we also included the following variables: the brood size as a categorical variable (as described above), the initial size variation (i.e. variation coefficient of 2-day body mass in the brood; a good proxy of hatching asynchrony (Rosivall et al., 2005)), year and the interaction of year with all variables, including the three-way interaction of experimental brood sex ratio and original brood sex ratio and year. Multicollinearity was not an issue, as VIF values for the initial models (without the interactive terms) were sufficiently small (nestling mortality model: all VIF <1.301, nestling recruitment model: all VIF <1.108; using function 'vif' from R package 'car' [Fox & Weisberg, 2019]). Fit of the initial models was validated visually by diagnostic plots based on quantile residuals generated by R package 'DHARMa' (using function 'simulateResiduals' Hartig, 2022). We did not find problems in the case of the mortality model. Though the diagnostic plots did not show serious problems in the case of the recruitment model either, the standard errors of the parameter estimates (Table S1a) were very high suggesting that the full model is not very reliable, therefore we repeated the analysis without the three-way interaction (see more details in the Results section).

We assessed the significance of the explanatory variables as described above. When none of the terms proved to be significant during the backward-stepwise elimination procedure, we obtained parameter estimates for the explanatory variables from single variable models (in case of interactive terms, the constituent main effects were also included). We present Wald chi-square tests.

3 | RESULTS

3.1 | Nestling development

We found that neither the original brood sex ratio nor the experimental brood sex ratio was related to the maximum body mass gain of the nestlings (Figure 3), and this was consistent in the two study years (Table 1). The interaction of the original brood sex ratio and the experimental brood sex ratio was not significant either (Table 1).

We found that nestlings grew faster in 2017 than in 2018 (Table 1, Figure 4a) and in smaller broods compared with larger broods (Table 1, Figure 4b). We also found that male nestlings grew faster than female nestlings (Table 1, Figure 4c). Relative 2-day body mass was positively related to maximum body mass gain that is the heavier the nestling was initially the faster it grew (Table 1). The strength of this relationship was dependent on the study year (Table 1, Figure 5). Post hoc tests revealed that the positive relationship of relative

FIGURE 3 Maximum body mass gain of cross-fostered collared flycatcher nestlings in relation to the sex ratio of their foster parents' (a) original and (b) experimental brood. Body mass gain was calculated as gram per hour and squared to ensure the normal distribution of the model residuals (see methods). The relationships were nonsignificant (see results). $N = 339$ nestlings.
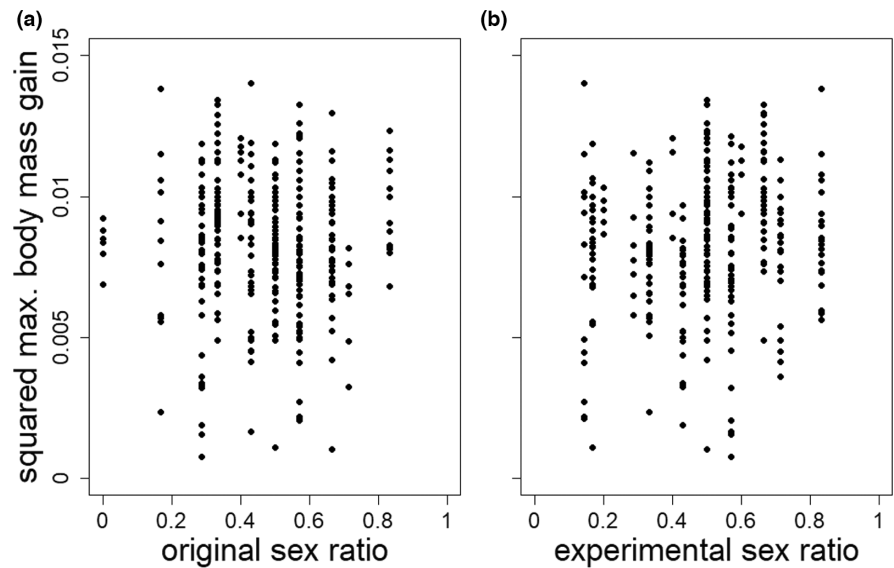

TABLE 1 The effects of brood sex ratios on growth (squared maximum body mass gain) in cross-fostered collared flycatcher nestlings

Fixed effects	F	df	p	Estimate ± SE (*10^{-3})
(intercept)				7.968 ± 0.198
Sex	**4.822**	**1, 292.1**	**0.029**	**0.204 ± 0.093**
Brood size	**15.510**	**1, 50.9**	**<0.001**	**0.757 ± 0.192**
Hatching rank	**45.217**	**1, 281.5**	**<0.001**	**3.418 ± 0.508**
Year	**20.942**	**1, 54.5**	**<0.001**	**0.865 ± 0.189**
Hatching rank*year	**6.890**	**1, 281.3**	**0.009**	**−1.339 ± 0.510**
Experimental sex ratio	0.244	1, 54.4	0.623	
Original sex ratio	0.002	1, 49.6	0.969	
Sex*year	1.807	1, 292.5	0.180	
Original sex ratio*year	1.025	1, 48.7	0.316	
Brood size*year	0.488	1, 49.6	0.488	
Experimental sex ratio*year	0.096	1, 50	0.758	
Original sex ratio*experimental sex ratio	0.077	1, 48.9	0.783	
Original sex ratio*experimental sex ratio*year	0.419	1, 46.1	0.521	
Random effects	χ^2	df	p	Variance
Original brood ID	**1.645**	**1**	**0.200**	**2.026×10^{-7}**
Foster brood ID	**40.345**	**1**	**<0.001**	**1.284×10^{-6}**
Residual				**2.523×10^{-6}**

Note: Parameters of the final model are highlighted in bold. F and p values for nonsignificant terms are derived from the model containing the respective term (in case of interactions, also the constituent main effects) and the terms that were retained in the final model. We present the parameter estimates and SEs only for the final model. In the 'lmer' function in R, we used the 'contr.sum' setting, therefore the parameter estimates for the categorical predictors (sex, brood size, year) show the first levels' (male, smaller, 2017, respectively) deviation from the grand mean. The value for the second level of predictor (female, larger, 2018, respectively) is the same but with opposite sign. Original brood ID and foster brood ID of the foster nestlings were included in the models as random factors and accordingly, degrees of freedom were approximated using Satterthwaite's formula. The importance of the random effects was tested using LRT tests. $N = 339$ nestlings.

2-day body mass with maximum body mass gain was significant in both years; however, the pattern was more pronounced in 2018 than in 2017 (2017: $F = 8.081$, $df = 1$, 165.6, $p = 0.005$ ($N = 199$ nestlings); 2018: $F = 43.353$, $df = 1$, 115.5, $p < 0.001$ ($N = 140$ nestlings); sex and brood size were retained in the post hoc models).

Foster brood ID explained a significant amount of individual variation in the maximum body mass gain of the nestlings, while original brood ID did not (Table 1).

3.2 | Nestling mortality

Nestling mortality occurred in 19.3% of the broods (11/57 broods). Neither the original brood sex ratio nor the experimental brood sex

ratio was related to nestling mortality (Table 2; Figure 6a,b). The interaction of the original brood sex ratio and the experimental brood sex ratio was not significant either (Table 2). The probability of nestling mortality was similar in the two study years and independent of brood size (Table 2). However, it was predicted by the extent of initial size variation, as a larger variation in 2-day body mass among the nestlings was associated with a higher probability of losing at least one nestling before fledging (Table 2, Figure 6c).

3.3 | Recruitment probability

The overall recruitment rate was 12.3% (44/357 nestlings). In the analysis of the recruitment rate, the three-way interaction
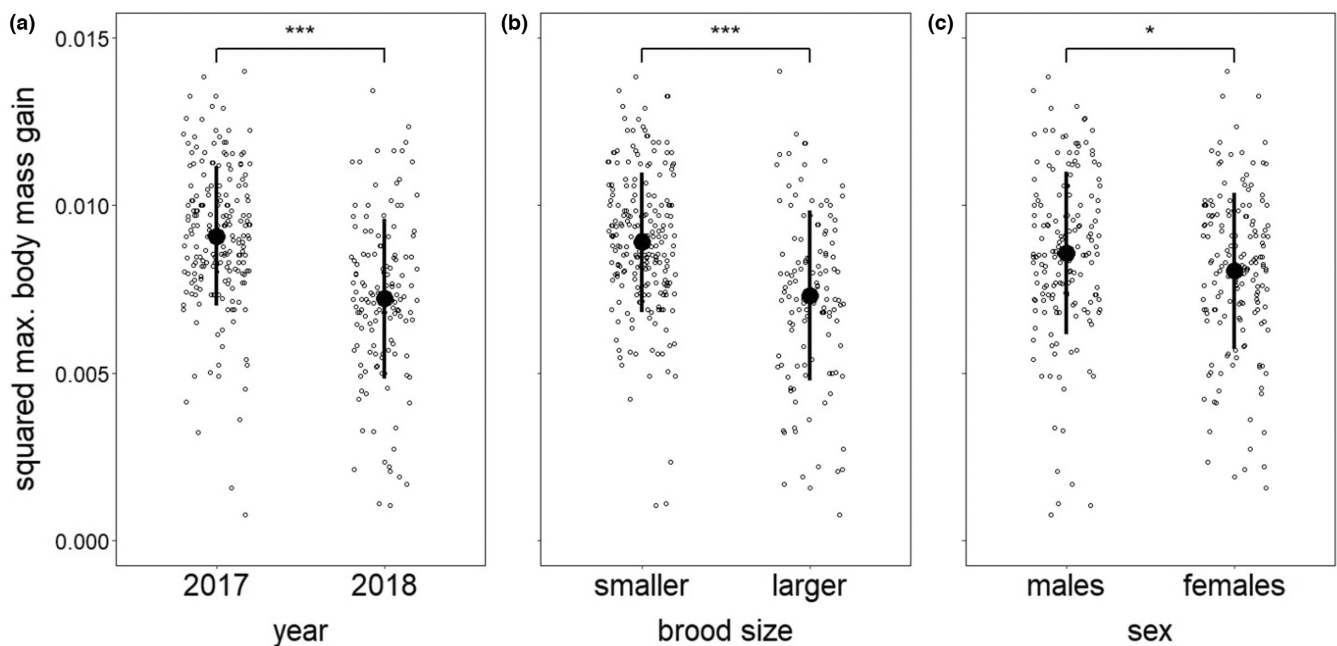

FIGURE 4 Squared maximum body mass gain of cross-fostered collared flycatcher nestlings in relation to (a) study year, (b) brood size and (c) sex (*** indicates $p < 0.001$ and * indicates $p < 0.05$; see results). Mean values (dots), SDs (whiskers) and point distributions are shown. $N = 339$ nestlings.
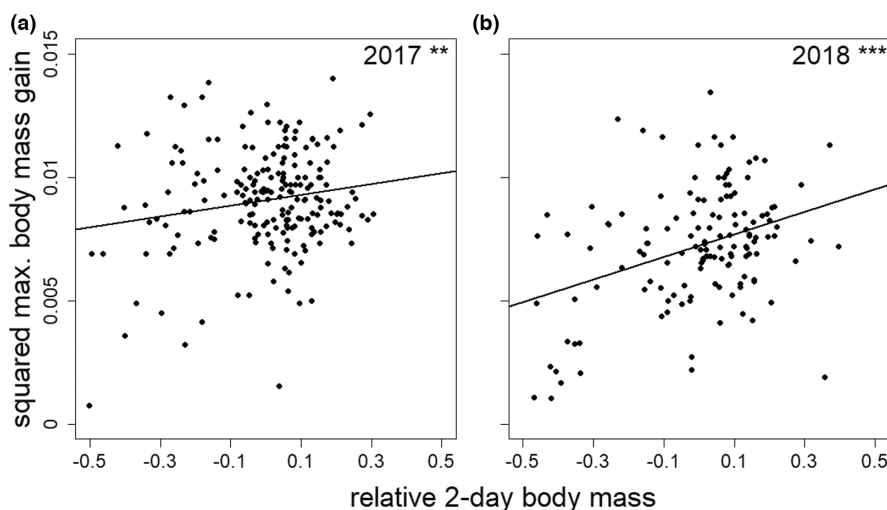

FIGURE 5 Squared maximum body mass gain of cross-fostered collared flycatcher nestlings in relation to their body mass on day 2 posthatch relative to brood average (approximates hatching rank) in the two study years separately (** indicates $p < 0.01$ and *** indicates $p < 0.001$; see results). $N = 199$ and 140 nestlings, respectively.

TABLE 2 The effects of brood sex ratios on the occurrence of nestling mortality in cross-fostered collared flycatcher broods

Explanatory variable	χ^2	df	p	Estimate $\pm$ SE
(intercept)				-4.678 ± 1.479
initial size variation	**5.872**	**1**	**0.015**	**0.157 ± 0.065**
Experimental sex ratio	2.188	1	0.139	
Brood size	1.926	1	0.165	
Original sex ratio	0.964	1	0.326	
Year	0.099	1	0.753	
Original sex ratio*experimental sex ratio	2.438	1	0.118	
Original sex ratio*year	1.417	1	0.234	
Experimental sex ratio*year	1.278	1	0.258	
Initial size variation*year	0.680	1	0.410	
Brood size*year	0.003	1	0.955	
Original sex ratio*experimental sex ratio*year	0.405	1	0.526	

Note: We used generalized linear model with binomial error distribution and logit link function. Terms retained in the final model are highlighted in bold. Wald χ^2 and p values for nonsignificant terms are derived from the model containing the respective term (in case of interactions, also the constituent main effects) and the significant terms that were retained in the final model. $N = 57$ broods.
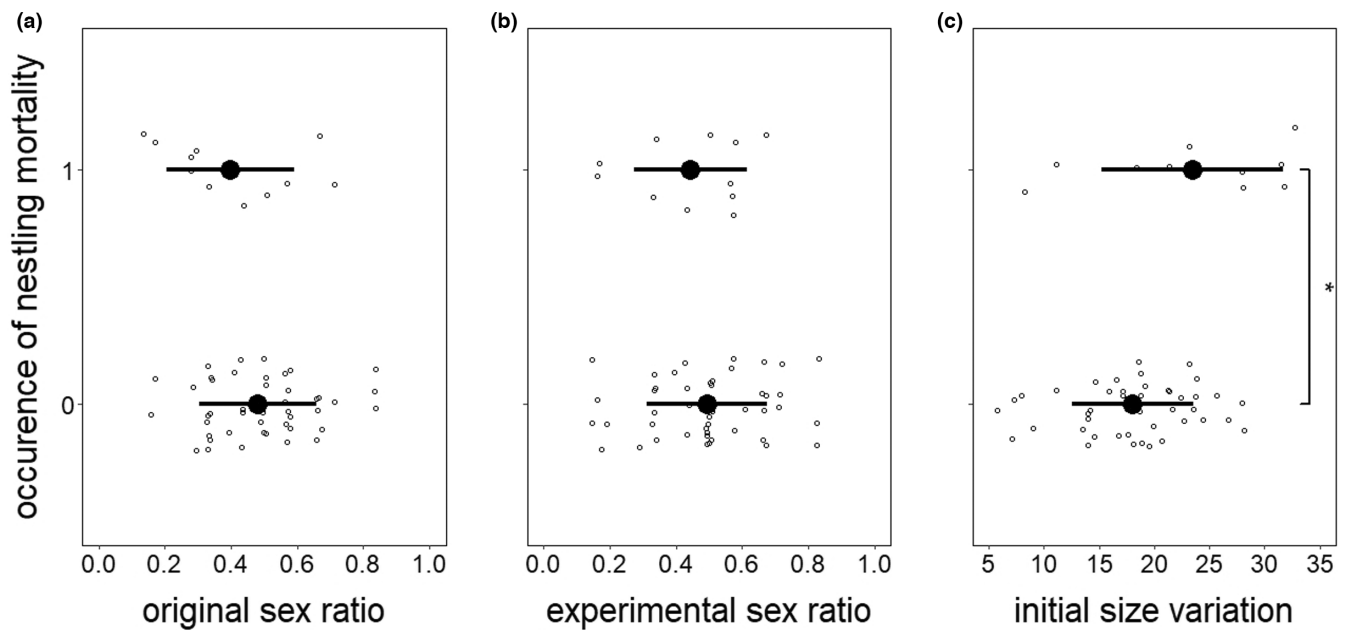

FIGURE 6 Occurrence of nestling mortality in cross-fostered collared flycatcher broods (coded binary at the brood level) in relation to the sex ratio of the foster parents' original (a) and experimental (b) brood, and initial size variation of the nestlings in the experimental brood (c). Initial size variation was estimated by the variation coefficient of 2-day nestling body mass. * indicates $p < 0.05$. Mean (dot), SD (whisker) and point distribution are shown. $N = 57$ broods.

of original brood sex ratio, experimental brood sex ratio and year was significant (Table S1a). However, the standard error of the estimate was very high, and no clear pattern was visible that could explain this interaction (Figure 7), suggesting that the significant effect was caused by the simultaneous effect of overparameterization and slight imbalances in the dataset. Therefore, we performed the analysis without the three-way interaction (Table S1b). After model simplification, all variables were nonsignificant (Table 3).

4 | DISCUSSION

Our study investigated the potential fitness consequences of different offspring sex ratios in a species where multiple earlier studies have found nonrandom brood sex ratios (Bowers et al., 2013; Ellegren et al., 1996; Rosivall et al., 2004; Szász et al., 2014). In our collared flycatcher study population, the reproductive success of males is more variable than that of females due to frequent extra-pair matings (Rosivall et al., 2009) and infrequent social polygyny
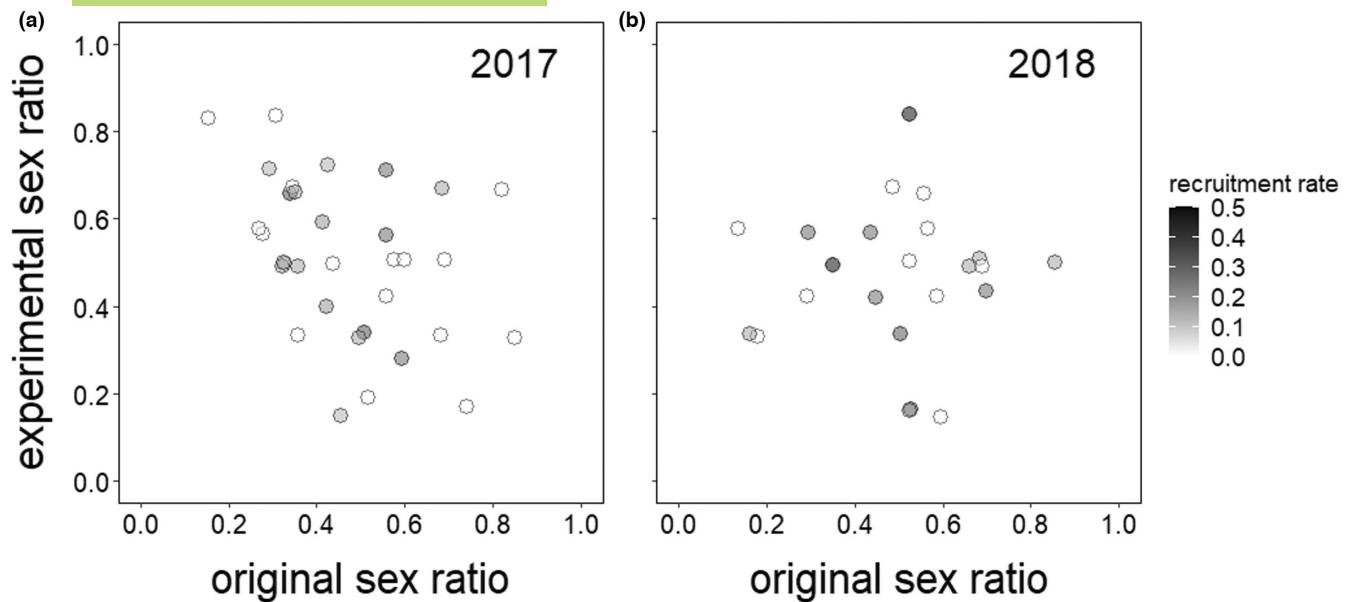
FIGURE 7 Recruitment rate of cross-fostered collared flycatcher broods (the number of nestlings that were recaptured as adults from all nestlings in the brood) in relation to the interaction between the experimental sex ratio and the original sex ratio of the brood in the two study years separately. $N = 33$ and 24 broods in 2017 and 2018, respectively.

TABLE 3 The effects of brood sex ratios on the recruitment rate of cross-fostered collared flycatcher broods

Explanatory variable	χ^2	df	p
Experimental sex ratio	0.259	1	0.611
Original sex ratio	0.024	1	0.878
Year	1.798	1	0.180
Brood size	0.245	1	0.621
Initial size variation	2.094	1	0.148
Brood size*year	1.831	1	0.176
Original sex ratio*year	0.385	1	0.535
Experimental sex ratio*year	0.211	1	0.646
Initial size variation*year	0.878	1	0.349
Original sex ratio*experimental sex ratio	0.128	1	0.721

Note: We used generalized linear model with binomial error distribution and logit link function. After the backward-stepwise simplification of the full model that did not contain the three-way interaction (see the Results section), none of the explanatory variables were retained in the model; therefore, Wald χ^2 and p values were derived from the model containing the respective main effect only, or in case of interactions, the interaction and the constituent main effects. $N = 57$ broods.

(Garamszegi et al., 2004; Herényi et al., 2012), however, male off-spring are more sensitive to early environmental conditions in terms of growth (Hegyi et al., 2011; Rosivall et al., 2010) and lifetime breeding performance (Szász et al., 2017). According to the theory of adaptive sex ratio adjustment, under these conditions, parents of better quality and with higher rearing capability should overproduce male offspring, and parents of inferior quality and with lower rearing capability should overproduce female offspring to maximize their fitness return. As follows, in the present cross-fostering experiment, we expected that nestlings (1) that are reared by parents who originally produced male-biased broods perform relatively better, (2) that develop in experimentally male-biased broods perform relatively

worse and (3) nestlings suffer less disadvantage in experimentally male-biased broods if their foster parents originally produced male-biased broods. However, none of these predictions were supported by our results on nestling growth, mortality and recruitment.

Our results are hard to compare to other studies on birds, because to our knowledge, no other studies investigated simultaneously the effect of the original and experimental sex ratio and their interaction in relation to offspring performance. Nonetheless, a study that investigated only the effects of original and experimental sex ratios (but not the interaction of these two), found that in the great tit, neither the original brood sex ratio nor the experimental brood sex ratio of the foster parents was related to

nestling performance (Nicolaus et al., 2009). Nicolaus et al. (2009) conducted the brood sex ratio manipulation on day 6 posthatch and created male-biased and female-biased broods by changing or leaving at least one original nestling in the experimental brood. This means that the nestlings spent ca. third of the nestling period with their original parents, and the foster parents cared for a mixture of related and unrelated nestlings. Consequently, in this study, the effects of the experiment could remain undetectable because of the late experimental manipulation and the entangled influence of the quality of the original and the foster parents. In our study, heritable variation and maternal effects do not seem to confound our results, as all foster parents cared for unrelated offspring only (that originated from two different broods), and in the analysis of nestling growth, the original brood ID (capturing the variance in nestling performance that was attributable to the quality of the original parents) was a nonsignificant random effect. In a Czech population of the collared flycatcher, Bowers et al. (2013) manipulated brood sex ratios already before hatching and all nestlings in a foster brood originated from different parents (Bowers et al., 2013). They found that those foster parents that fledged heavier broods, originally produced male-biased broods (Bowers et al., 2013); therefore, the primary brood sex ratio pattern was suggested to be adaptive. It seems that our results contradict this finding, though we used a more sensitive measure of nestling development (i.e. in contrast to a point estimate of final body mass, we used the maximum speed of body mass gain). The two studies are difficult to compare for theoretical and statistical reasons. Bowers et al. (2013) aimed to analyse how brood sex ratio depends on parental quality, thus used the original brood sex ratio as the response variable, and fledging body mass of the foster offspring and the experimental brood sex ratio as explanatory variables. By contrast, we aimed to reveal how the fitness payoff of parents depends on brood sex ratio, thus used the nestling growth rate as the response variable, and original brood sex ratio, experimental brood sex ratio and their interaction as explanatory variables.

If we try to find an explanation for the lack of the expected effects in our study, at least three lines of nonexclusive explanations arise. First, it is possible that the sex difference in the effects of early environment on growth trajectories is not due to a sex difference in overall energy requirement but a sex difference in energy allocation strategy. Energy allocation to body size versus immune function at the end of the nestling period was suggested to differ between male and female nestlings in the great tit (Tschirren et al., 2003) and the blue tit (Dubiec et al., 2006), though no sex difference was found in a Polish population of the collared flycatcher (Wilk et al., 2007). Second, it is also possible that the sex difference in the energy requirement of the nestlings is small and the effects of our experiment are undetectable in relatively food-rich years. The study years were relatively food-rich as indicated by the faster development of male nestlings compared with female nestlings in both study years, a pattern that has been found only under favourable conditions in our study population (Hegyi et al., 2011; Rosivall et al., 2010). The idea that fitness

consequences of offspring sex ratios may be year-dependent is supported by a study on red deers (Kruuk et al., 1999). Third, if male nestlings have a higher energy requirement, it is possible that in male-biased broods, the nestlings beg more intensely than in female-biased broods. Accordingly, foster parents of experimentally male-biased broods may have increased their food delivery rate and in this way, compensated for the surplus of males and masked the developmental differences between experimentally male-biased and female-biased broods.

This parental compensation scenario raises the possibility that foster parents directly paid the costs or gained the benefits of the brood sex ratio experiment, and not indirectly through offspring performance, that is their own future reproductive value was influenced. There is an example for this in the tammar wallaby, where the interaction between the sex of the foster offspring and the sex of the original offspring had no effect on the survival and the body mass of the foster offspring (Robert et al., 2010), while those mothers that fostered the sex opposite of what they originally produced were less likely to give birth in the year following the experiment than mothers that fostered the same sex (Schwanz & Robert, 2016).

Finally, another possible explanation for the lack of brood sex ratio effects is that the development of the nestlings is influenced by multiple variables that act simultaneously and have impacts of different magnitudes. The most important determinant of nestling development is probably the availability of food. Even if the parents do not need to compete for the food they deliver because of good year quality, within the brood, the nestlings may still compete among each other for the food they are provisioned with. In a species with sexually size-monomorphic nestlings like the collared flycatcher, the level of this competition is likely to depend on the number and the hatching hierarchy of the nestlings. Accordingly, study year, brood size, hatching rank and hatching asynchrony may have a different order of magnitude of impact on nestling development compared with brood sex ratio.

In accordance with this final explanation, we found a negative relationship between brood size and the body mass gain of the nestlings. This is in line with earlier experimental results in our study population, where experimental brood enlargement resulted in a slower body mass gain of nestlings compared with experimental brood reduction (Rosivall et al., 2010; Szöllősi et al., 2007) and also with results of other species where increased brood size resulted in smaller size at fledging (for example, in blue tits; Blondel et al., 1998; Fargallo & Merino, 1999; Råberg et al., 2005), great tits (Hőrak, 2003; Rytkönen & Orell, 2001), spotless starlings (*Sturnus unicolor*; [Gil et al., 2008]). The initial size disadvantage of late-hatched nestlings also had a negative effect on nestling growth, which is consistent with earlier results on hatching asynchrony in our study population (Rosivall et al., 2005; Szöllősi et al., 2007). Nestlings gained body mass slower and late-hatched nestlings experienced more disadvantages in 2018 than in 2017. Both study years were relatively food-rich, but the breeding density was higher in 2018 than in 2017 (216 collared flycatcher broods in 2018 and 177 collared flycatcher broods in 2017 in our respective

nest-box plots), and this may explain the nestling growth patterns. In addition to these, male nestlings gained body mass faster than female nestlings, which might be attributable to the high food availability, because male nestlings have a higher growth potential under favourable conditions (Rosivall et al., 2010). In broods, where the initial size variation among the hatchlings was more pronounced, nestling mortality was more likely to occur, which is a commonly observed consequence of hatching asynchrony (Stenning, 1996).

To sum up, we did not obtain experimental evidence for brood sex ratio patterns being adaptive in a species, where sex-dependent sensitivity to rearing conditions had been convincingly established, and brood sex ratio had been found to be correlated with several parental and environmental characteristics. We studied the adaptive value of sex ratio adjustment by looking at the performance of the offspring because early life conditions have been shown to have sex-dependent effects in collared flycatchers. Another approach for the future is to investigate the residual reproductive value of the parents as a function of their brood sex ratio. To better understand the selective forces shaping offspring sex ratio, it is important to conduct experimental studies similar to ours on a number of species, because since the theory of adaptive sex ratio adjustment has been formulated, the fitness consequences of nonrandom offspring sex ratio patterns have remained uninvestigated in most sex ratio studies.

AUTHOR CONTRIBUTIONS

Eszter Szász: Formal analysis (supporting); investigation (equal); methodology (equal); visualization (equal); writing – original draft (lead); writing – review and editing (lead). **Fanni Sarkadi:** Data curation (lead); formal analysis (lead); investigation (equal); visualization (equal); writing – review and editing (equal). **Eszter Szöllősi:** Funding acquisition (supporting); investigation (equal); methodology (equal); writing – review and editing (equal). **Renáta Kopena:** Investigation (equal); writing – review and editing (equal). **János Török:** Investigation (equal); writing – review and editing (equal). **Balázs Rosivall:** Conceptualization (lead); data curation (supporting); formal analysis (supporting); funding acquisition (lead); investigation (equal); methodology (equal); supervision (lead); writing – review and editing (lead).

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST

PEER REVIEW

DATA AVAILABILITY STATEMENT

ETHICAL APPROVAL

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.