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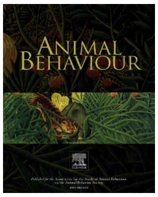

Songbird brood sex ratio varies in response to male attractiveness and rearing conditions

Simone Santoro [a, b, *], María Losada [c, d], David Canal [e], Carlos Camacho [c], Jesús Martínez-Padilla [f], Alfredo Sánchez-Tójar [g, h, i], Jaime Potti [c]

[a] Department of Integrated Sciences, Faculty of Experimental Sciences, University of Huelva, Huelva, Spain
[b] Department of Natural Sciences and Environmental Health, University of South-Eastern Norway, Bø, Norway
[c] Department of Ecology and Evolution, Estación Biológica de Doñana (CSIC), Seville, Spain
[d] Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland
[e] Department of Evolutionary Ecology, National Museum of Natural Sciences (MNCN-CSIC), Madrid, Spain
[f] Department of Biological Conservation and Ecosystem Restoration, Pyrenean Institute of Ecology (IPE-CSIC), Jaca, Spain
[g] Department of Evolutionary Biology, Bielefeld University, Bielefeld, Germany
[h] CNC-UC, Centre for Neuroscience and Cell Biology, University of Coimbra, Coimbra, Portugal
[i] CIBB, Centre for Innovative Biomedicine and Biotechnology, University of Coimbra, Coimbra, Portugal

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Empirical evidence shows that brood sex ratios can be influenced by environmental factors and reproductive success–related parental traits. The Trivers–Willard hypothesis (TWH) predicts condition-dependent adjustment of offspring sex ratios and has been extended to suggest that females mated to more attractive males will bias offspring sex ratios towards sons, as sons that resemble their fathers could yield greater fitness returns through increased grandoffspring production. Although extensive research has explored the effect of male attractiveness on sex allocation, its interplay with environmental conditions is often overlooked. This study examines how brood sex ratios respond to both male attractiveness and annual rearing conditions (ARC; proxied by annual breeding success) within the framework of the TWH. Using long-term data from 2759 molecularly sexed nestlings of pied flycatchers, *Ficedula hypoleuca*, ringed between 1997 and 2018 (with 643 brood sex ratios determined from eight breeding seasons between 1997 and 2011) and by tracking lifetime fledgling production through the 2023 breeding season, we found support for sex ratio adjustment as predicted by the TWH. Male attractiveness and ARC positively affected the proportion of males in the broods. These associations were partially context-dependent, with each factor becoming influential only when the other was unfavourable. Analyses of nestling mortality before genetic sexing at day 13 after hatching showed that nestling mortality was more frequent in female-biased broods, decreased with favourable rearing conditions and increased with male attractiveness. Importantly, excluding broods with early nestling mortality left the main sex ratio conclusions unchanged. In addition, we did not find statistical evidence for an association between male attractiveness or ARC and offspring's lifetime reproductive success. Our findings suggest that sex allocation is influenced by poor rearing conditions, sexually selected traits and their interplay. Further research is needed to confirm this relationship and to clarify the fitness consequences for sons and daughters.

In his foundational work, Fisher (1930) showed that any deviation from a 1:1 sex ratio results in frequency-dependent selection favouring the rarer sex, thereby stabilizing equal parental investment in sons and daughters. Although this equal allocation principle explains the widespread occurrence of balanced sex ratios, subsequent theory has argued that deviations may be adaptive under certain conditions. Specifically, Hamilton (1967) challenged Fisher's assumption that a 1:1 sex ratio is always evolutionarily stable, suggesting that facultative adjustments could be adaptive.

Sex ratio adjustments are driven by diverse factors that operate at both environmental and parental levels (West, 2009).

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* Corresponding author.
E-mail address: simone.santoro@usn.no (S. Santoro).

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Environmental factors can modify sex ratios independently of parental strategies by, for example, differentially affecting the survival or development of male and female embryos (Kruuk, Clutton-Brock, Rose, & Guinness, 1999; Post et al., 1997; Weladji et al., 2003). Moreover, when brood sex ratio is quantified among surviving nestlings rather than at conception, sex-biased nestling mortality can shift the observed brood sex ratio independently of parental allocation (Daan et al., 1996; Santoro et al., 2015). However, parental traits can also be key determinants. According to the Trivers–Willard hypothesis (TWH; Trivers & Willard, 1973), parents in prime condition may favour the production of the more costly sex, whereas additional good genes or Fisherian mechanisms may cause females mated to attractive males to produce more sons (Burley, 1981, 1986; Wang et al., 2018), particularly in species where females exert greater control over offspring sex (Krackow, 1995).

However, a recent systematic review and meta-analysis indicates that although there is a slight, statistically significant tendency for attractive males to sire a higher proportion of sons, the overall support for such facultative adjustment is weak and sensitive to publication bias, with significant effects reported only for specific traits such as ornamentation and body size (Booksmythe et al., 2017). Theoretical models (e.g. Booksmythe et al., 2013; Fawcett et al., 2007, 2011; Pen & Weissing, 2000) suggest that strong sex ratio adjustment in response to male attractiveness may evolve only under particular genetic and ecological conditions, namely when the heritable benefits of attractiveness are mainly limited to sons, female choice is costly, recurrent deleterious mutations (biased mutation) maintain variation in male traits and the costs of sex ratio manipulation are low. Such adjustment can, in turn, weaken sexual selection on male traits.

In this study, we investigate how parental quality, rearing conditions and their interaction shape offspring sex ratio adjustments. Previous work supports this framework: Kruuk, Clutton-Brock, Rose, and Guinness (1999) found that the association between maternal dominance and a male-biased brood sex ratio appears only under favourable conditions and weakens when the population density is high or resources are scarce. Similarly, Nager et al. (1999) showed that poor maternal condition lowers male survival and leads to sex ratios biased towards daughters.

Building on these findings, we hypothesized that favourable rearing conditions and high paternal attractiveness promote the production of a greater proportion of sons, but their effects depend on one another. If resources are abundant, females are expected to bias the brood sex ratio towards sons as all offspring can attain high quality, and sons should accrue greater reproductive returns (Trivers & Willard, 1973). Under these conditions, the added benefit of paternal attractiveness via heritable traits (good genes) and enhanced parental care (Burley, 1986; Kokko, 2001) would be modest, resulting in only a slight additional male bias. If resources are scarce, however, paternal quality could become critical for offspring survival and the future mating success of sons. Consequently, females might be more likely to bias the brood sex ratio towards sons when paired with an attractive male, given the substantially higher potential fitness returns.

Research on the collared flycatcher, *Ficedula albicollis*, has shown that brood sex ratios can be adjusted based on the father's phenotype, specifically the size of their sexual ornament (Ellegren et al., 1996). Our study focuses on a closely related species, the pied flycatcher, *Ficedula hypoleuca*. This small, insectivorous, migratory songbird shows facultative polygyny, with considerable interannual variation in the frequency of social polygyny (Canal et al., 2020; Santoro et al., 2022). Upon arrival at the breeding grounds, males secure nest sites, attract females in various ways, including through their ornaments (e.g. forehead patch), and contribute to the parental care of their offspring (Canal et al., 2021). However, the extent of this contribution can vary, especially from monogamous to bigamous males, as the latter often provide less care to secondary broods (Lifjeld & Slagsvold, 1989; Lundberg & Alatalo, 1992; Potti & Montalvo, 1993). This variation in male attractiveness and parental investment, combined with fluctuating environmental conditions, offers an excellent opportunity to test hypotheses regarding brood sex ratio adjustment (Szász et al., 2017). Cross-fostering experiments conducted on the congeneric collared flycatcher show that poor rearing conditions have a greater negative impact on the size of male nestlings compared to that in females (Rosivall et al., 2010), significantly influencing their future lifetime reproductive success (Szász et al., 2017).

Herein, we assess the predictions of TWH by examining how the interplay between rearing conditions and parental quality (i.e. male attractiveness) affects brood sex ratio adjustment using long-term monitoring data from a pied flycatcher population. We use yearly breeding success, calculated as the mean number of fledglings across all broods in the population, as a proxy for the annual rearing conditions (ARC). Because brood sex ratios in our system are quantified at day 13 after hatching, we examine whether sex-biased nestling mortality before this age can distort the sex ratio. Specifically, we compare sex ratios between broods with and without early nestling losses to test whether male or female offspring die disproportionately; assess whether mortality varies with ARC, paternal attractiveness or habitat type and verify that excluding broods with early nestling mortality does not alter the main patterns of sex ratio variation. In addition, we assess the TWH's core assumption that fitness returns to parents differ between offspring sexes by comparing lifetime fitness (that is, the number of fledglings produced over a lifetime) between sons and daughters as functions of their father's attractiveness and their rearing conditions, thereby testing whether the observed fitness differences align with the sex ratio analysis.

METHODS

Study Population and Field Procedures

Data used in this study were obtained from a long-term study (started in 1984) of a European pied flycatcher population breeding in nestboxes around La Hiruela (central Spain; ca. 41°N, 3°W; 1200–1300 m above sea level), with reliable records available from 1987. The study area contains 237 nestboxes distributed approximately every 20 m (SD = 14.1) across a mature deciduous forest (mainly Pyrenean oak, *Quercus pyrenaica*; $N = 156$ nestboxes) and a nearby (at ca. 1 km) coniferous plantation (mainly Scots pine, *Pinus sylvestris*; $N = 81$ nestboxes). Across the eight seasons with molecular sexing (1997, 1998, 2005–2009 and 2011), an average of 54% (SD = 11%) of the nestboxes were occupied annually, with very similar rates observed in both habitats.

During the breeding season, which typically spans from mid-April (with the arrival of first males) to early July (when the last nestlings fledge), we regularly checked the nestboxes to record the stage of nest building, the laying date (that is, the day the first egg in the clutch is laid), clutch size, hatching date and brood size (number of fledglings at 13 days of age). Parents were trapped inside the nestboxes while feeding nestlings, ringed (if necessary) and weighed (±0.1 g), and their tarsus length (±0.1 mm; distance between bending points; Alatalo & Lundberg, 1986) and wing length were measured (±0.5 mm). The white forehead patch of black-and-white European *Ficedula* flycatchers is attractive for females and its size is an honest signal of male quality (Gustafsson et al., 1995). In this population, the size of this plumage patch is also a predictor of extra-pair paternity and social polygyny, and it is associated with earlier breeding, which increases the chances of social polygyny within the breeding season (Canal et al., 2021). We computed forehead patch size as the product of its height (±0.01 mm) and width (±0.01 mm). Hereafter, this heritable trait (Potti & Canal, 2011) is used as a proxy of male quality/attractiveness. Breeders ringed as nestlings were of exactly known age. In contrast, unringed individuals (immigrants) were aged as young (first year, 1 year old) or adult (at least 2 years old) based on their plumage traits (Karlsson et al., 1986; Lundberg & Alatalo, 1992; Potti & Montalvo, 1991a).

Nestling mortality between hatching and day 13 averaged 20.5% (SD = 33.5%; N = 4532 nests, 22 495 hatchlings) over the long-term study period (1987–2023). For each brood, we recorded both the total number of hatchlings and the number of nestlings that died before day 13, which allowed us to calculate brood-level mortality (presence/absence, number of losses and proportion of dead vs. alive). Our annual capture-recapture program allowed us to track the fate of all ringed nestlings recruited into the breeding population in subsequent years. This enabled us to assess the lifetime reproductive success for each individual, defined as the total number of fledglings produced over its lifetime. The studied population shows strong natal and breeding site fidelity, with recruitment rates averaging 14% and reaching up to 22% in some years, among the highest reported for the species (Canal et al., 2014; Potti et al., 2013; Potti & Montalvo, 1991b). Nearly all adults resighted in subsequent years bred within 150 m of their previous nest site (Montalvo & Potti, 1992); adults not resighted may have emigrated or died. Natal dispersal is limited: approximately 27% of locally fledged recruits bred in a nearby monitored patch within the study area (that is, between the adjacent deciduous forest and the coniferous plantation, ca. 1 km apart) for their first breeding attempt, whereas the remaining 73% bred in their natal patch; both ring recoveries and intensive searches for singing males suggest that breeding outside the study area is rare (Camacho et al., 2015). There is no familial resemblance in dispersal propensity (Camacho et al., 2015), and on average, 48% of males (N = 1,991) and 57% of females (N = 2,136) were immigrants (i.e. previously unringed breeders) over the whole study period (1984–2023). Given these patterns, it is reasonable to assume that a substantial proportion of surviving fledglings recruit locally within the study population, although unobserved emigration cannot be excluded.

Over the eight breeding seasons used for the brood sex ratio analysis (1997, 1998, 2005–2009 and 2011), we molecularly sampled 3428 13-day-old nestlings from 728 broods. Among these, 3090 nestlings (90.1%: 1508 males and 1582 females) from 643 broods had complete data and were used in the sex ratio analyses, whereas 2796 nestling (81.6%: 1415 males and 1381 females) had complete data for the lifetime fitness analysis (more details in Canal et al., 2014; Potti et al., 2002). For each nestling, a blood sample (<50 μL) was taken from the brachial vein and preserved in pure ethanol for subsequent DNA-based sex determination (Griffiths et al., 1998; Potti et al., 2002). These ringed and molecularly sexed fledglings were subsequently tracked via our annual monitoring program throughout the 2023 breeding season, enabling us to quantify each individual's lifetime number of fledglings well beyond the maximum reported lifespan for pied flycatchers (11.9 years; Fransson et al., 2023).

Statistical Analyses

All analyses were performed in R version 4.3.3 (R Core Team, 2024). Generalized linear mixed models (GLMMs) were fitted using the 'glmmTMB' function in the glmmTMB package version 1.1.12 (Brooks et al., 2017). All continuous predictors were standardized to a zero mean and unit SD. This enhances the comparability of effect sizes among predictors within a model and across models and allows main effect estimates to be interpreted at average predictor values. We validated the models' assumptions and assessed their goodness-of-fit using the 'simulateResiduals' function in the DHARMa package version 0.4.7 (Hartig, 2021), ensuring that residual diagnostics met the required standards. In addition, multicollinearity among predictors was examined using the 'check_collinearity' function in the performance package version 0.15.1 (Lüdecke et al., 2021). We found no multicollinearity among predictors, and residual diagnostics confirmed that the models' assumptions were met.

We prepared and quality checked the accompanying data and code repository by following the Society for Open, Reliable, and Transparent Ecology and Evolutionary Biology (SORTEE) guidelines for data and code quality control in ecology and evolutionary biology (Pick et al., 2025).

Testing Predictions of TWH on Brood Sex Ratio

We evaluated the TWH by modelling brood sex ratio as a function of male attractiveness (forehead patch size), ARC (proxied by the mean number of fledglings across all broods in a given year) and their interaction, thereby assessing whether the effect of paternal attractiveness on brood sex ratio varies with population-wide rearing conditions. The habitat of birth (i.e. deciduous vs. coniferous forest) and hatching date were included as covariates to account for environmental and temporal variation, and a random intercept for year accounted for potential nonindependence among observations from different years. Models were fitted with a binomial error distribution and a logit link. Because the relative importance of the predictors was uncertain, we applied a multimodel inference approach (Burnham & Anderson, 2002). Specifically, we constructed a candidate set of 20 GLMMs comprising all nonempty subsets of five predictors (male attractiveness, ARC, their interaction, habitat and date), with the constraint that the interaction term was included only when both main effects were present. Model selection was based on the corrected Akaike information criterion ($\mathrm{AIC_c}$) using the MuMIn package version 1.48.11 (Barton, 2024), and model averaging was performed to obtain robust estimates that accounted for model selection uncertainty. To interpret the male attractiveness × ARC interaction, we conducted a conditional effects analysis at the fifth and 95th percentiles of ARC, computing the conditional slopes and their SEs directly from the model's predictor estimates and variance–covariance matrix using the delta method.

Assessing Potential Bias from Nestling Mortality

Because the brood sex ratio was quantified at day 13 after hatching, we evaluated whether early nestling losses biased the observed sex ratios. First, we modelled brood sex ratio as a function of whether any nestlings died before day 13. Then, we modelled early nestling mortality at the brood level against ARC, male attractiveness and habitat and evaluated the male attractiveness × ARC interaction. Finally, we repeated the brood sex ratio analysis after excluding broods with early mortality to verify robustness. Models were fitted with a binomial error distribution using a logit link, and year was included as a random intercept.

Testing Predictions of TWH on Sons' and Daughters' Lifetime Fitness

Since adaptive sex ratio adjustment is driven by differential fitness returns, we linked our predictors to both sex ratio adjustment and fitness outcomes by evaluating, separately, how sons' and daughters' lifetime fitness (that is, the number of fledglings produced over an individual's lifespan) is associated with male attractiveness, ARC and their interaction. Lifetime fitness was calculated using individuals marked as nestlings between 1997 and 2018, with fledgling production tracked through the 2023 breeding season. The majority of these offspring (99.9%) did not recruit into the breeding population and had, therefore, zero lifetime reproductive success (LRS; 1319 males and 1268 females vs. 96 males and 113 females with nonzero LRS). However, neither zero-inflated nor hurdle models provided adequate fits across different distribution families; therefore, we adopted a two-stage approach. First, we used a binomial GLMM to model whether offspring achieved any lifetime direct fitness (0 vs. >0). The predictors included male attractiveness, ARC and their interaction as well as hatching date and habitat of birth, with a random effect for the nestbox of birth nested within each year. Second, we used a lognormal GLMM with the same set of predictors for offspring with nonzero lifetime direct fitness.

Ethical Note

All captured individuals were handled following standardized ringing protocols. Adults were captured while feeding nestlings using a conventional, harmless spring trap (Friedman et al., 2008). The handling time of adult birds was brief (mostly <15 min) to reduce stress. We followed all legal requirements to ensure animal welfare, including positive assessments by the ethical committees of our research institutes and approval from the autonomous regions (Comunidad de Madrid and Comunidad Autónoma de Castilla-La Mancha). Specifically, capture and ringing were authorized by Doñana Biological Station-CSIC and the Autonomous Communities of Madrid and Castilla-La Mancha. Ethical approval was granted by the CSIC Ethical Committee (refs. PAC05-006-2, CGL2006-07481/BOS, CGL2009-10652, CGL2011-29694 and CGL2014-55969-P) and the Andalusian Committee of Animal Experimentation (ref. 2011_03 to J.P.) under Spanish and European animal protection laws.

RESULTS

Model-averaged estimates (Fig. 1) indicated clear positive effects of male attractiveness and ARC on brood sex ratio (expressed as the proportion of sons). The top-ranked model (model 17; Table 1) confirmed this pattern: broods showed an almost 1:1 sex ratio when males were more attractive ($\beta = 0.092$, 95% CI = 0.02 to 0.164, $P = 0.012$; Fig. 1a and b) and ARC was favourable ($\beta = 0.101$, 95% CI = 0.025 to 0.178, $P = 0.009$), but shifted towards a female bias when males were less attractive and ARC was poor. Based on the same model, although the overall interaction between male attractiveness and ARC was not statistically significant ($\beta = -0.056$, 95% CI = -0.126 to 0.014, $P = 0.115$; Fig. 1c and d), conditional effects analysis revealed that the effect of male attractiveness was more substantial under poor rearing conditions ($\beta = 0.216$ at the fifth percentile) than under favourable conditions ($\beta = 0.001$ at the 95th percentile; $P = 0.007$). Broods in the coniferous forest showed statistically significantly lower sex ratios than those in the deciduous forest ($\beta = -0.169$, 95% CI = -0.032 to -0.011, $P = 0.036$).

Analyses of early nestling mortality showed that broods with mortality had more female-biased sex ratios than broods without mortality ($\beta = -0.195$, 95% CI = -0.356 to -0.033, $P = 0.018$). The probability of mortality decreased with more favourable ARC ($\beta = -0.266$, 95% CI = -0.391 to -0.141, $P < 0.001$) and increased with paternal attractiveness ($\beta = 0.172$, 95% CI = 0.031 to -0.313, $P = 0.017$), whereas the interaction between paternal attractiveness and ARC was not statistically significant ($\beta = -0.007$, 95% CI = -0.146 to -0.131, $P = 0.919$). Mortality did not differ significantly between habitats ($\beta = 0.196$, 95% CI = -0.047 to 0.44, $P = 0.114$). Importantly, when broods with early mortality were excluded, the main sex ratio results remained largely unchanged (father attractiveness: $\beta = 0.102$, 95% CI = 0.02 to -0.184, $P = 0.014$; ARC: $\beta = 0.082$, 95% CI = 0 to -0.164, $P = 0.051$; habitat: $\beta = -0.197$, 95% CI = -0.377 to -0.017, $P = 0.032$; interaction: $\beta = -0.077$, 95% CI = -0.156 to 0.002, $P = 0.057$).

In the analysis of sons' and daughters' lifetime fitness that assessed whether individuals produced any descendants (0 vs. >0), we detected no statistically significant effects of father attractiveness, ARC or their interaction for either sex. In the follow-up analysis of offspring with nonzero reproductive success, none of these predictors influenced the number of fledglings produced. The only statistically significant effect was that daughters hatched later in the season had higher LRS ($\beta = 0.137$, $P = 0.001$), whereas all other predictors were statistically nonsignificant (see the Supplementary material for full model outputs).

DISCUSSION

Our results revealed that male attractiveness was positively associated with the proportion of sons per brood in years with adverse rearing conditions (low ARC), suggesting that fluctuating rearing conditions can modulate the association between paternal sexual traits and sex allocation in pied flycatcher broods. These findings indicate that brood sex ratios were close to parity when rearing conditions were favourable and fathers were of higher quality (larger forehead patch) but shifted towards a female bias when rearing conditions were poor or fathers were less attractive. Only a few sex allocation studies have tested predictions regarding the fitness of sons and daughters separately. However, we found no statistically significant effect of male attractiveness, rearing conditions or their interaction on offspring lifetime fitness, calling into question the mechanism predicted by TWH.

Our long-term study accounts for multiple confounding factors, revealing that, in line with the TWH, females paired with less ornamented males are more likely to overproduce daughters in this population. Because brood sex ratios were measured at day 13 after hatching, we explicitly tested whether differential early nestling mortality could explain the observed patterns. Although broods with early mortality were more female-biased, and mortality itself was associated with both ARC and paternal attractiveness, excluding such broods left the main sex ratio results virtually unchanged. Although broods without mortality could still form a nonrandom subset, the consistency of the results indicates that early mortality alone is unlikely to explain the patterns we report. Overall, these findings suggest that sex-biased nestling mortality was not an important driver of the observed association between paternal attractiveness, rearing conditions and brood sex ratio.

The TWH has received substantial support in many vertebrate studies, particularly those of birds, linking sex ratio adjustments to male attractiveness (Burley, 1981; Dreiss et al., 2005; Ellegren et al., 1996; Korsten et al., 2006; Polo et al., 2004; Rosivall et al., 2004; Sheldon et al., 1999) or other parental quality indicators, such as survival and body condition (Rathburn & Montgomerie, 2004; Stauss et al., 2005; Svensson & Nilsson, 1996). Indeed, a recent meta-analysis of the role of male attractiveness on sex

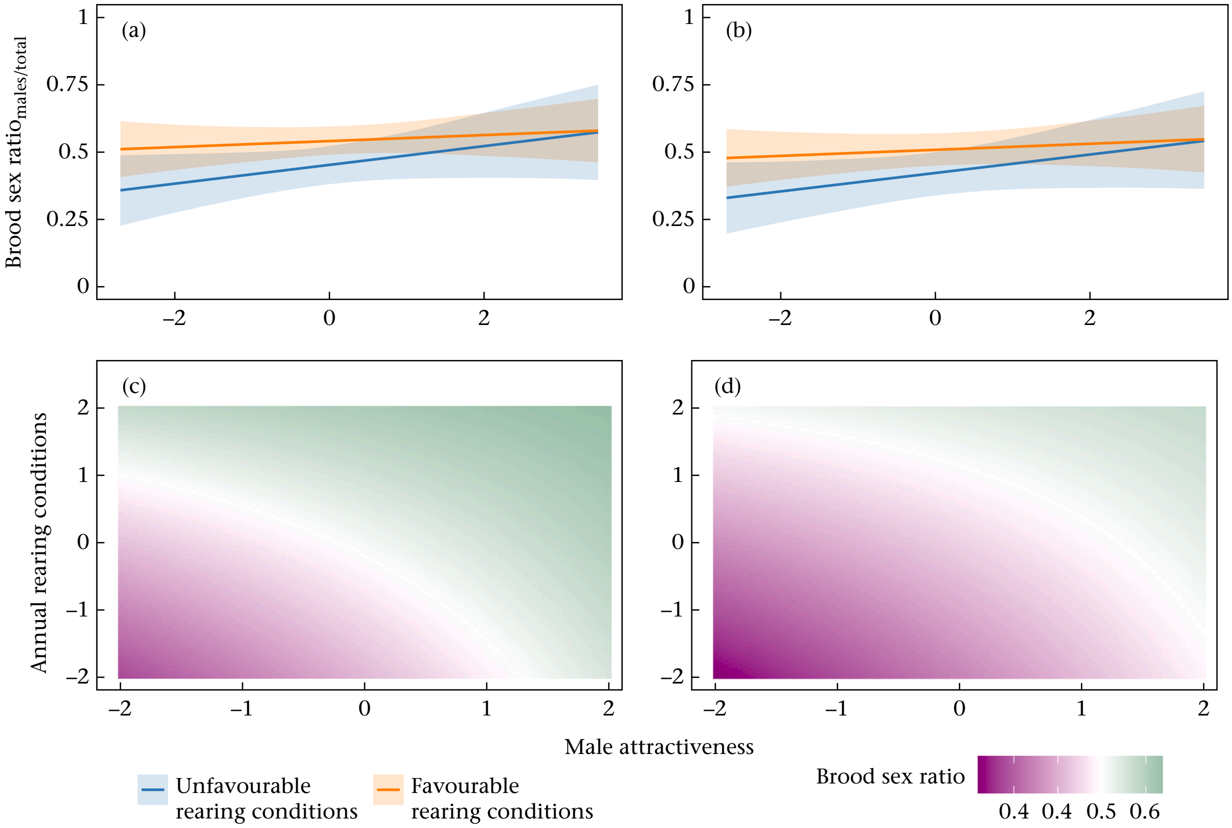

Figure 1. Model-averaged results illustrating how brood sex ratio (proportion of sons ± 95% CI) varies with male attractiveness (forehead patch size) and annual rearing conditions (ARC). (a) and (b) show the independent effects of male attractiveness and ARC on brood sex ratio in deciduous and coniferous forests, respectively, under unfavourable (blue) and favourable (orange) rearing conditions. (c) and (d) show predictions of brood sex ratio in deciduous and coniferous forests as a function of the interaction between male attractiveness and ARC, showing that the effect of one variable is stronger when the other is low. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Model selection table ranking candidate binomial generalized linear mixed models predicting brood sex ratio (proportion of sons) as a function of male attractiveness (fatherA), annual rearing conditions (ARC), habitat of birth and hatching date

Model	FatherA	ARC	Habitat	Date	ARC:fatherA	*df*	AIC$_c$	Δ	Weight
17	0.092	0.101	+		−0.056	6	1893.500	0.000	0.256
12	0.089	0.107	+			5	1893.943	0.443	0.205
20	0.093	0.106	+	0.029	−0.055	7	1895.124	1.625	0.114
18	0.090	0.112	+	0.031		6	1895.488	1.988	0.095
13	0.090	0.098			−0.054	5	1895.871	2.371	0.078
6	0.087	0.103				4	1896.176	2.676	0.067
7	0.098		+			4	1897.458	3.959	0.035
8		0.122	+			4	1897.780	4.280	0.030
19	0.090	0.097		−0.001	−0.054	6	1897.908	4.408	0.028
14	0.087	0.104		0.002		5	1898.205	4.706	0.024
15	0.096					3	1899.226	5.726	0.015
16	0.099		+	0.017		5	1899.355	5.855	0.014
2		0.126	+	0.024		5	1899.511	6.011	0.013
3		0.118				3	1899.832	6.332	0.011
9	0.096			−0.009		4	1901.203	7.703	0.005
10		0.118		−0.004		4	1901.849	8.349	0.004
4			+			3	1902.573	9.073	0.003
11						2	1904.106	10.606	0.001
1			+	0.008		4	1904.568	11.068	0.001
5				−0.016		3	1905.979	12.479	0.000

The columns for fatherA, ARC, date and ARC:fatherA report the estimated regression coefficients for these predictors when included in the model, whereas a ‘+’ in the habitat column indicates that the corresponding predictor is included. Candidate models include all nonempty subsets of predictors, with the interaction between ARC and fatherA (ARC:fatherA) included only when both main effects are present. The null model (with only an intercept and a random effect of year) is included ($df = 2$). AIC$_c$: Akaike information criterion corrected for small sample size; Δ: difference in AICc relative to the best model.

allocation in birds pointed to sexual ornaments (such as the forehead patch size of male pied flycatchers) and body size as the most relevant drivers of sex ratio adjustments (Booksmythe et al., 2017). However, some studies report contradictory findings, even within the same model species (Korsten et al., 2006; Leech et al., 2001; Mazuc et al., 2003; Nomi et al., 2015; Pryke & Rollins, 2012; Radford & Blakey, 2000; Sheldon & Ellegren, 1996). These discrepancies likely reflect small effect sizes and considerable biological and methodological heterogeneity among studies, as suggested by previous reviews (Booksmythe et al., 2017; West et al., 2002). Another potential reason is that these studies may have overlooked the combined role of parental quality and environmental conditions. In this regard, our study suggests that when rearing conditions are optimal, the impact of male quality on offspring sex ratio diminishes, highlighting the importance of considering variation in environmental conditions in analyses of sex ratio adjustment.

Several theoretical hypotheses and empirical studies have explored how individual and environmental factors influence sex allocation in birds and mammals (Clark, 1978; Emlen et al., 1986; Lessells & Avery, 1987; Taylor & Bulmer, 1980). However, the interaction between the fathers' quality or attractiveness and rearing conditions has received less attention. In this study, we paired paternal forehead-patch size (a proxy for male quality) with yearly average breeding success, a direct measure of the ARC, and found that higher ARC and greater paternal attractiveness both bias broods towards sons. Although our findings align with theoretical expectations of sex ratio adjustments, they do not support our predictions on the differential lifetime fitness of sons and daughters. The fitness consequences of sex allocation in vertebrates remain inadequately explored (Jan, 1998; Komdeur & Pen, 2002; Nager et al., 1999; West, 2009). As West (2009, p. 190) noted, '… one of the biggest problems for the field of sex allocation is a lack of studies demonstrating the fitness consequences of sex ratio adjustments … '. This study is one of the few to simultaneously test the TWH and the predictions of sex-related variation in offspring's lifetime fitness in response to male attractiveness. Although brood sex ratios were skewed towards daughters when males were less attractive and rearing conditions were poor, we detected no corresponding lifetime fitness advantage for either sex. One possible explanation for this is compensatory parental care. Sanz (2001) experimentally reduced forehead patches in pied flycatchers and showed that males perceived as 'less attractive' increased their feeding effort and reared offspring with longer tarsi, suggesting that unattractive males may offset potential disadvantages for their offspring. Overall, sex allocation effects typically account for only a tiny fraction of brood sex ratio variation (Booksmythe et al., 2017; West, 2009), making any downstream differences in son versus daughter fitness inherently difficult to detect. Furthermore, in our two-stage modelling, we focused solely on recruitment probability and fledgling counts and found that few offspring achieved a nonzero LRS. As a result, subtler sex-specific fitness differences arising later in life (e.g. variation in adult survival, extrapair success or grandoffspring production; Santoro et al., 2022) may have gone undetected, potentially obscuring any adaptive payoff of sex ratio adjustment in our study.

In conclusion, our study provides important insights into how environmental rearing conditions and paternal quality influence sex ratio adjustments in pied flycatchers. Although we showed that low male attractiveness and poor rearing conditions can lead to a shift in brood sex ratio towards daughters, the mechanistic basis of this association remains to be established, especially given our results that falsified the theoretical predictions of the TWH regarding the fitness of sons and daughters. Our findings suggest complex sex allocation dynamics, and we can only speculate on the underlying mechanisms behind the unexpected lifetime fitness outcomes for sons and daughters. Moreover, although our findings align with some of the TWH predictions, they underscore the complexity of sex ratio control mechanisms, including potential influences from primary sex ratios and differential post-laying mortality. Future research should focus on elucidating the underlying mechanisms of sex ratio control, exploring how male traits impact female choice and sex allocation under variable environmental conditions. Such studies would enhance our understanding of sex allocation dynamics and their implications for reproductive success across various bird species.

Author Contributions

Simone Santoro: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **María Losada:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **David Canal:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition. **Carlos Camacho:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition. **Jesús Martínez-Padilla:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition. **Alfredo Sánchez-Tójar:** Data curation. **Jaime Potti:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition.

Data Availability

Data and code for this study are available as Supplementary Material.

Declaration of Interest

The authors have no competing interests to declare.

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Supplementary Material

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