



# Facultative and persistent offspring sex-ratio bias in relation to the social environment in cooperatively breeding red-winged fairy-wrens (*Malurus elegans*)

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## Abstract

Females should facultatively bias offspring sex ratio when fitness returns vary among sexes. In cooperative breeders, where individuals help raise others' young, overproducing the philopatric sex will be adaptive when helpers are absent, whereas overproducing the dispersive sex may be adaptive to reduce intrasexual competition. Thus, fitness returns are expected to vary with the social environment. However, any offspring sex-ratio biases may also result from consistent among-female differences (e.g. quality) and/or environmental variables (e.g. food availability). Yet, few studies have disentangled facultative from persistent biases. We investigated offspring sex-ratio biases in relation to the social environment in cooperatively breeding red-winged fairy-wrens (*Malurus elegans*). Repeated observations of the same females over nine years allowed for disentanglement of facultative from persistent biases. Females without help did not overproduce daughters, despite female helpers being associated with higher fledgling survival (resource enhancement hypothesis). Instead, females without helpers facultatively overproduced sons—the slower dispersing sex—thereby ensuring long-term helper availability. Furthermore, offspring sex ratio was not biased towards the rarer sex of helpers present in the group or population (resource competition hypothesis). However, females with sex-biased helping produced similarly skewed offspring sex ratios. This among-female association may not be surprising, because helpers are previous seasons' offspring. Thus, in addition to facultative responses to prevailing social conditions, we found evidence for persistent biases among females. This could potentially explain previous evidence for resource competition/enhancement that have typically been interpreted as facultative responses, highlighting the need for a within-female approach to better understand the adaptiveness of sex-ratio biases.

## Significance statement

Under certain conditions, females may benefit from producing a biased offspring sex ratio, but evidence for such effects in vertebrates is weak and inconsistent. Here, using observations of the same females under different social conditions, we show that cooperatively breeding red-winged fairy-wrens facultatively biased offspring sex ratio towards sons when living in pairs, thereby ensuring the availability of a workforce to assist in raising future offspring. However, biased offspring sex ratio patterns may also be the result of consistent differences among females. Indeed, we also found evidence for such patterns and suggest that this could be an explanation for previous findings which are often interpreted as facultative responses.

**Keywords** *Malurus elegans* · Cooperative breeding · Local resource competition hypothesis · Local resource enhancement hypothesis · Within-subject centring

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## Introduction

Females are expected to invest equally in the production of sons and daughters when both sexes have similar reproductive value (Fisher 1930). However, when fitness returns differ between the sexes, theory predicts that selection should favour females that facultatively bias offspring production

towards the sex that will maximize parental fitness (Hamilton 1967; Trivers and Willard 1973; Charnov 1982; Frank 1990). Fitness returns may vary among the sexes when one sex is costlier to produce than the other, which is likely to vary with resource availability, or when future parental benefits differ due to variance in lifetime fitness between the sexes (Frank 1990; Sheldon 1998; Cockburn et al. 2002).

In many cooperative breeders—where individuals help raise others' offspring—fitness returns vary among the sexes, because one sex is more likely to delay dispersal and help raise the next brood than the other (Cockburn et al. 1998). When the presence of helpers enhances their fitness, females are predicted to overproduce the more helpful and often less dispersive sex (local resource enhancement hypothesis, Gowaty and Lennartz 1985; Emlen et al. 1986; Lessells and Avery 1987). However, a large number of helpers in the group can also increase competition among group members, in which case females are predicted to overproduce the more dispersive sex (local resource competition hypothesis, Clark 1978). Females are thus expected to facultatively bias the sex ratio of offspring, who may later become helpers, depending on the sex of helpers present in their group, i.e. their social environment. For instance, in laughing kookaburras (*Dacelo novaeguineae*), where breeding pairs are assisted by male and female helpers, the presence of male helpers has no effect on parental fitness, but female helpers depress productivity (Legge 2000). Consistent with the local resource competition hypothesis, females overproduced sons when living in groups consisting of mainly female helpers (Legge et al. 2001). Although largely unknown, mechanisms through which such facultative adjustment could occur include asynchronous follicular development, selective resorption or sex specific fertilization (Pike and Petrie 2003).

Sex ratio theory has repeatedly made exquisitely accurate predictions, particularly in invertebrates (Hamilton 1967; Charnov 1982; Seger and Stubblefield 2002; West 2009). However, in birds and mammals, empirical evidence for predictions concerning sex allocation has proved less successful (Clutton-Brock 1986; Clutton-Brock and Iason 1986; Hewison and Gailard 1999; Cockburn et al. 2002; Ewen et al. 2003; West et al. 2005; Uller 2006). Despite numerous studies reporting observations of biased offspring sex ratios in several vertebrate taxa (e.g. reptiles—Uller et al. 2006; birds—Pryke et al. 2011; fish—Kahn et al. 2013; mammals—Allainé et al. 2000), only a limited number of studies provide evidence for facultative offspring sex ratio adjustment (Komdeur et al. 1997; Nager et al. 1999; Sheldon et al. 1999; Pryke and Griffith 2009). Furthermore, results are often difficult to reproduce or fail to match clear theoretical predictions (Radford and Blakey 2000; Cockburn et al. 2002; Komdeur and Pen 2002; Cockburn and Double 2008; Kingma et al. 2011). Rather than a plastic

response of the female to specific conditions, observed offspring sex ratio biases may also be explained by consistent differences among individuals (e.g. Reznick et al. 2000) or by environmental variables directly. For example, initial findings in red deer (*Cervus elaphus*) that dominant females produced more sons were explained as a facultative mechanism to increase a female's fitness, because maternal dominance affected their son's breeding success more than their daughter's (Clutton-Brock et al. 1984). However, later work found that the observed sex ratio bias produced by dominant females declined with increasing population density and winter rainfall, environmental variables that affected both female condition and selective loss of male fetuses, suggesting that multiple mechanisms can affect offspring sex ratio in a single population (Kruuk et al. 1999). Thus, it remains uncertain if and to what extent birds and mammals *facultatively* bias the sex ratio of their offspring. To disentangle whether observed offspring sex ratio biases are the result of a plastic facultative response rather than a persistent bias, a within-individual approach can be used whereby changes in offspring sex ratio can be examined as a function of changes with the predictor of interest (Komdeur et al. 1997; Westerdahl et al. 2000; Oddie and Reim 2002). Studies examining associations between the social environment and offspring sex ratio have typically interpreted biases as facultative responses to resource enhancement or resource competition (Allainé et al. 2000; Nunn and Pereira 2000; Clarke et al. 2002; Ewen et al. 2003; Dickinson 2004; Silk and Brown 2008; Woxvold and Magrath 2008; Varian-Ramos et al. 2010; Canestrari et al. 2012; Luthermann et al. 2014), but persistent biases have not been considered in this context. Therefore, it remains unclear whether there is evidence for facultative adjustments.

Here, we examine whether cooperatively breeding red-winged fairy-wrens (*Malurus elegans*) bias their offspring sex ratio depending on their social environment, i.e. the number and sex of the helpers in the group. Repeated observations of the same females under varying ecological and social conditions allow us to distinguish whether offspring sex ratio biases are the result of within-individual facultative responses or due to persistent among-individual differences. In *M. elegans*, both sexes are philopatric and delay dispersal for at least one year to help raise the next brood (Rowley et al. 1988). When dispersal occurs, it is to a nearby territory, but females disperse slightly further (median distance females vs. males: 2 vs. 1 territory distance, Russell and Rowley 2000) and on average earlier (median age females vs. males: 2 vs. 3 years, Brouwer et al. 2020) than males. Previous work has shown that offspring provisioning rates of all group members varied with the sex of helpers present in the group: with an increasing number of male helpers in the group, each individual reduced its offspring provisioning rates (load-lightening). In contrast,

with an increasing number of female helpers in the group, each individual provisioned at a constant rate (additive care; Brouwer et al. 2014; Macleod and Brouwer 2018). As a result, with an increasing number of female, but not male helpers, nestlings received more food, grew larger and had higher post fledgling survival (Brouwer et al. 2014). We thus predict that when help would be most needed, i.e. in the absence of helpers, females should facultatively bias offspring sex ratio towards daughters (local resource enhancement hypothesis, Gowaty and Lennartz 1985; Emlen et al. 1986; Lessells and Avery 1987; Griffin et al. 2005; Table 1: prediction 1). However, a larger number of helpers in the group can also increase competition among group members (Clark 1978), and due to the limited availability of mates and breeding vacancies in *M. elegans* (Rowley et al. 1988), this is expected to be stronger between same-sex compared to opposite-sex helpers. Thus, we predict that with an increasing number of same-sex helpers in the group, females should facultatively bias offspring sex ratio towards the sex opposite of those helpers already present in the group (local resource competition hypothesis, Table 1: prediction 2a). Competition in the presence of female helpers is expected to be particularly strong (Table 1: prediction 2b), because an increasing number of female helpers in the group has been shown to be associated with reduced helper survival (Lejeune et al. 2016). Similarly, at the population level, females are expected to overproduce the rarer sex. This effect is expected to be particularly pronounced with a high number of females (Table 1: prediction 2c), because in contrast to males who habitually sire offspring as a helper, females are largely dependent on the availability of a territory to breed (Brouwer et al. 2011). In addition, because males are 9% heavier than females when fully grown (Rowley et al. 1988), we also test whether equal investment in sons and daughters at the end of parental care would result in a persistent bias towards cheaper females (Fisher's hypothesis, Fisher 1930, Table 1: prediction 3). Finally, we also examine potential facultative and/or persistent effects of poor environmental conditions during and among breeding seasons.

## Methods

### Study area and data collection

Data were collected in Smithbrook Nature Reserve (34° 20' S, 116° 10' E) in south-west Western Australia during nine breeding seasons (Oct–Jan of 2008–2016). The 95-ha nature reserve largely consists of Eucalypt wet forest with a dense understory (for more detailed description: Rowley et al. 1988). The main study area comprised 58–70. *elegans* territories of which > 99% of the adult birds were individually colour-banded. Those territories were visited at least

**Table 1** Overview of the main hypotheses explaining variation in offspring sex ratios in cooperative breeders, with their general and specific predictions for *M. elegans*. Hypotheses may predict both a persistent offspring sex ratio bias at the population level, or predict a plastic facultative offspring sex ratio bias within females

| Hypothesis   | General prediction   | Prediction for <i>M. elegans</i>   |
|--|--|--|
| 1 Local resource enhancement (Gowaty and Lennartz 1985; Emlen et al. 1986; Lessells and Avery 1987): bias towards the more helpful sex | 1 Facultative bias towards the helpful sex in the absence of helpers   | 1 Facultative bias towards daughters in the absence of helpers, because offspring benefit more from female helpers (Brouwer et al. 2014)   |
| 2 Local resource competition (Clark 1978): bias towards the dispersive sex   | 2a Facultative bias towards the dispersive sex with an increasing number of helpers in the group<br>2c Persistent bias towards the rarer sex | 2a Facultative bias towards the sex opposite of the sex of helpers present, due to the limited availability of mates and breeding vacancies (Rowley et al. 1988)<br>2b Stronger facultative bias with an increasing number of female helpers compared to male helpers, because a larger number of female helpers in the group is associated with reduced helper survival (Lejeune et al. 2016)<br>2c Persistent bias towards daughters with an increasing number of adult males, and towards sons with an increasing number of adult females in the population |
| 3 Fisher's (Fisher 1930): equal investment in the production of males and females  | 3 Persistent bias towards the cheaper sex when sexes differ in size  | 3 Persistent bias towards daughters, who have 9% lower body mass, because with equal investment, the cheaper sex would be more abundant at the end of parental care  |

fortnightly to collect data on group composition, survival and breeding activity. In addition, in another ~30 territories surrounding the main area on average ~80% of the birds were individually colour-banded and nest searching was done opportunistically. Social status of group members was determined from behavioural observations, variation in plumage and age (Rowley et al. 1988; Russell and Rowley 2000), with each group comprising a pair-bonded male and female and 0–8 subordinate male and/or female helpers (mean  $\pm$  SD =  $0.9 \pm 1.0$  male and  $0.6 \pm 0.8$  female helpers per group). Once located, nests were checked at least twice a week to collect data on the egg laying date, clutch size, number of hatchlings and the number of fledglings. Females only rarely raised two successful broods within a season but may initiate up to four clutches within a season due to high predation rates (~70%) of complete clutches/broods. Nestlings were blood sampled when at least two days old and any abandoned clutches and unhatched eggs were collected for genotyping. Nestlings were banded when eight days old with a metal ring from the Australian Bird and Bat Banding Scheme and a unique colour-band combination. All blood (ca. 15  $\mu$ L) and tissue samples were stored in 1 mL of 100% ethanol and stored at room temperature. DNA sexing of nestlings was performed using P2/P8 primers (Griffiths et al. 1998) and the scoring of the genotypes was done blindly. For a subset of individuals that survived to be sexed based on plumage characteristics, the accuracy of the DNA sexing methods could be verified, which showed that only one out of 517 individuals (0.19%) was incorrectly sexed. Since starvation is extremely rare, the near complete sampling of eggs and nestlings means that the sex ratio data is close to the primary sex ratio.

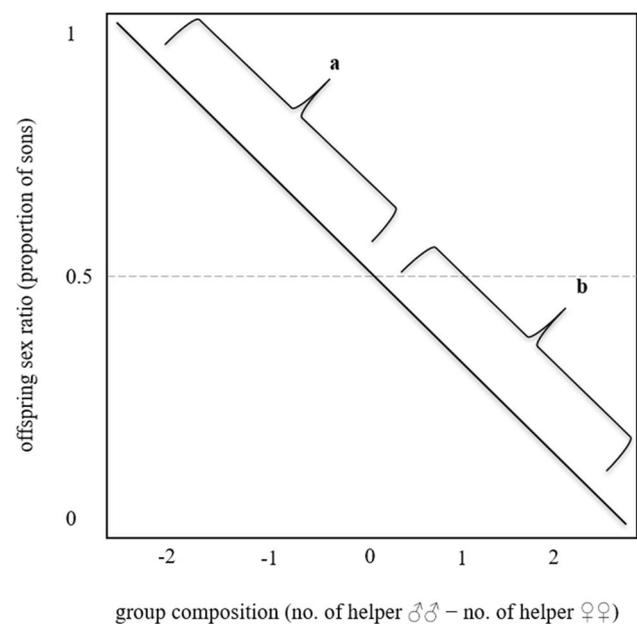
### Statistical analyses

Offspring sex ratio was defined as the proportion of male nestlings in each brood. To test our prediction under Fisher's hypothesis (Table 1: prediction 3), we examined whether offspring sex ratio deviated from 50/50 using a binomial test on the complete dataset which contained 730 broods (range 1–13 broods per female, 1597 nestlings) from 253 unique breeding females.

To test for facultative and/or persistent offspring sex-ratio biases, two separate generalized linear mixed models (GLMM) were fitted based on subsets of the complete dataset. In each model, the number of sons versus the number of daughters per brood was fitted as a binomial response using a logit link function. The first GLMM examined whether females without helpers were more likely to produce daughters compared to females with helpers (local resource enhancement hypothesis, Table 1: prediction 1) by including whether helpers were present in the group (yes/no). In addition, this model examined whether females biased

offspring sex ratio towards the rarer sex in the population (local resource competition hypothesis, Table 1: prediction 2c) by including the number of adult males (range 93–130) and adult females (range 77–150) present in the population. The dataset contained 650 broods (1434 nestlings) from 229 unique breeding females with known breeding experience.

The second GLMM examined whether those females living in groups (174 breeding females producing 1119 nestlings from 493 broods) biased their offspring sex ratio towards daughters in the presence of male helpers and towards sons in the presence of female helpers by including 'group composition' as a predictor (local resource competition hypothesis, Table 1: prediction 2a). Under the local resource competition hypothesis, there will be simultaneous effects of both the number and sex of helpers on offspring sex ratio (i.e. a stronger response is expected when multiple same-sex rather than a single helper is present). To simultaneously test this effect of number and sex of the helpers, a new predictor 'group composition' was created, defined as the number of helper males – the number of helper females provisioning the brood. Negative values of this predictor indicate female-biased groups, whereas positive values indicate male-biased groups (Fig. 1). This predictor also allowed us to test the prediction that competition will be stronger for female-biased groups compared to male-biased



**Fig. 1** The predicted association between group composition (no. of helper males – no. of helper females provisioning the brood) and the proportion of sons in *M. elegans* broods under the local resource competition hypothesis (Table 1). Negative values represent groups that are female-biased, whereas positive values represent groups that are male-biased. We predict that the effect of local competition will be stronger for female-biased groups, thus the slope of a > slope of b. The horizontal grey dashed line indicates equal offspring sex ratio

groups (Table 1: prediction 2b), by comparing the slopes of the group composition effects for female-biased (group composition =  $\leq 0$ ) and male-biased groups (group composition =  $\geq 0$ , Fig. 1: a vs. b).

In both models, year and breeding female identity were used as random intercepts to account for non-independence of the data. We also examined the effects of poor years (i.e. the annual average number of fledglings per territory), breeding female breeding experience (first time breeder: yes/no), and facultative or persistent response to diminishing breeding conditions (lay date) by including these as fixed effects in the models. Relative lay date for each clutch was calculated as the deviation from the median lay date for that year, thereby accounting for year-effects in phenology.

Repeated observations of the same breeding females over several years (mean number of clutches per breeding female = 2.89, range = 1–13, Fig. S1) with varying group sizes and compositions allowed us to disentangle whether biases in offspring sex ratio are due to facultative within-female phenotypically plastic responses or persistent differences between females, using a mixed modelling approach called ‘within-subject centring’ (van de Pol and Wright 2009). With this method, we split up the ‘helper presence’, ‘group composition’ and ‘lay date’ variables into two predictors: the mean of each variable per breeding female indicates the persistent (i.e. between-female) effect, whereas the annual deviation of the mean value per female indicates the facultative (within-female) response.

## Model fitting

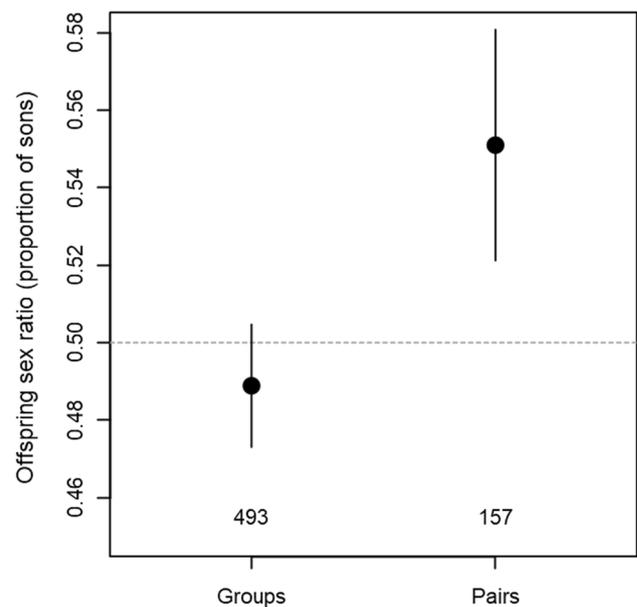
To assess the relative importance of facultative and persistent sex ratio biases in *M. elegans* and compare how models with the centred predictors differ from those with the main effects, we used a model selection approach. For both GLMMs (see above), we selected the most parsimonious models using Akaike’s Information Criterion (AIC), corrected for sample size (AICc, Akaike 1973), with models that are better supported by the data resulting in lower AICc values. Models were constructed by including all possible combinations of predictors, with the exception that within-female centred and main effects were not included simultaneously. We reported a summary of the model selection results including the top models within  $\Delta\text{AICc} < 2$  of the best supported model, the null and the full model (out of 400 and 50 models respectively, see Tables S1, S2 for full model output). All explanatory variables were transformed to z-scores before including them in the model. Collinearity was examined using variance inflation factor analyses (VIF), which indicated very low collinearity among predictors (all  $\text{VIF} < 1.5$ , Zuur et al. 2010). Statistical analyses were performed in R version 4.1.2 (R Development Core Team 2021) using RStudio (RStudio Team 2021). Models were created

using the package ‘MuMIn’ (Bartón 2020) and run using the package ‘lme4’ (Bates et al. 2014). Within-subject centring was performed using the package ‘Climwin’ (van de Pol et al. 2016).

## Results

### Local resource enhancement- and competition hypothesis

In contrast to the local resource enhancement hypothesis (Table 1, prediction 1), females did not bias offspring sex ratio towards daughters in the absence of helpers (Fig. 2). Interestingly, the opposite pattern was evident: females without help were more likely to bias their offspring production towards sons (Fig. 2). Indeed, model selection results showed that including the helper presence predictor was supported by the data (Table 2, model 1 vs. model 25). Furthermore, disentangling the within- from the between-female effect showed that this was likely a facultative response, because a model including the within-female predictor, but not the between-female predictor, was better supported than the null model (Table 2, model 2 and 48 vs. model 25). This effect was received strong supported by the data, because ‘helper presence’ or the within-female predictor of ‘helper presence’ was included the top 24 models and overall these predictors received 0.82 model weight (Table S1). There was no evidence that additional variation in offspring sex



**Fig. 2** The mean ( $\pm$ SE) proportion of sons in *M. elegans* broods in relation to whether females lived in groups or pairs. The grey dashed line indicates 50/50 offspring sex ratio. Numbers in the bottom of the plot indicate the number of broods

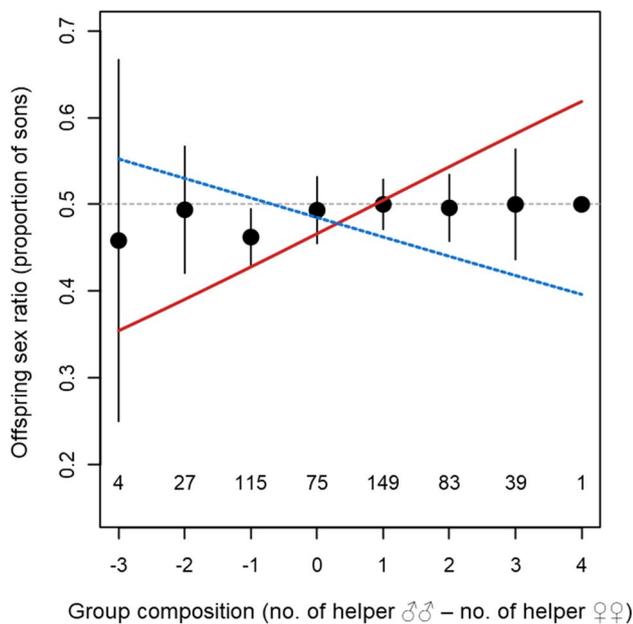
**Table 2** Summary of model selection results investigating the effect of helper presence (yes = female with helpers, no = female without helpers) on offspring sex ratio in *M. elegans* broods ( $n = 650$ ). Predictors were included by their main effect and by using within-subject centring, allowing to distinguish between facultative within-female (within) and persistent between-female (betw) effects. Shown are standardized coefficients ( $z$ -scores) with their standard errors (SE). Predictors in the top model of which 95% CI do not overlap zero are shown in bold. Predictor variables that were not fitted in a model are indicated by “-”. No. adult (fe)males: total number of adult (fe)males in the population; breeding exp: breeding experience of breeding female; No. of fl: annual number of fledglings per territory in the population. See Table S1 for complete model output (400 models)

| Model      | Intercept   | Helper presence <sub>within</sub> | Helper presence <sub>betw</sub> | Helper presence | Helper presence <sub>betw</sub> | Helper presence | Helper presence | No. adult females | No. adult males | Lay date <sub>within</sub> | Lay date <sub>betw</sub> | Lay date    | Breeding exp <sup>a</sup> | No. fledglings | $\sigma^2_{year}$ | $\sigma^2_{female ID}$ | df | $\Delta AIC_c$ |
|------------|-------------|-----------------------------------|---------------------------------|-----------------|---------------------------------|-----------------|-----------------|-------------------|-----------------|----------------------------|--------------------------|-------------|---------------------------|----------------|-------------------|------------------------|----|----------------|
| 1          | 0.02 ± 0.08 | -                                 | -                               | -               | <b>-0.12 ± 0.06</b>             | -               | -               | -                 | -               | -                          | -                        | -           | -                         | -              | 0.02 ± 0.14       | 0.05 ± 0.23            | 4  | 0.00           |
| 2          | 0.02 ± 0.08 | -0.11 ± 0.06                      | -                               | -               | -                               | -               | -               | -                 | -               | -                          | -                        | -           | -                         | -              | 0.02 ± 0.15       | 0.06 ± 0.24            | 4  | 0.42           |
| 3          | 0.02 ± 0.08 | -                                 | -                               | -               | -0.12 ± 0.06                    | -               | -               | -                 | -               | -0.06 ± 0.08               | -                        | -           | -                         | -              | 0.02 ± 0.14       | 0.06 ± 0.24            | 5  | 0.86           |
| 4          | 0.02 ± 0.08 | -                                 | -                               | -               | -0.13 ± 0.06                    | -               | -               | -                 | -               | -                          | -                        | -           | -0.06 ± 0.06              | -              | 0.02 ± 0.15       | 0.06 ± 0.24            | 5  | 0.99           |
| 5          | 0.02 ± 0.08 | -0.11 ± 0.06                      | -0.07 ± 0.06                    | -               | -                               | -               | -               | -                 | -               | -                          | -                        | -           | -                         | -              | 0.02 ± 0.14       | 0.05 ± 0.23            | 5  | 1.11           |
| 6          | 0.01 ± 0.08 | -0.11 ± 0.06                      | -                               | -               | -                               | -               | -               | -                 | -               | -0.07 ± 0.06               | -                        | -           | -                         | -              | 0.02 ± 0.14       | 0.06 ± 0.24            | 5  | 1.12           |
| 7          | 0.02 ± 0.08 | -                                 | -                               | -               | -0.12 ± 0.06                    | -               | -               | -                 | -               | 0.05 ± 0.05                | -                        | -           | -                         | -              | 0.02 ± 0.14       | 0.05 ± 0.23            | 5  | 1.34           |
| 8          | 0.02 ± 0.07 | -0.11 ± 0.06                      | -                               | -               | -                               | -               | -0.07 ± 0.07    | -                 | -               | -                          | -                        | -           | -                         | -              | 0.02 ± 0.13       | 0.06 ± 0.24            | 5  | 1.66           |
| 9          | 0.02 ± 0.07 | -                                 | -                               | -               | -0.12 ± 0.06                    | -               | -0.04 ± 0.07    | -                 | -               | -                          | -                        | -           | -                         | -              | 0.02 ± 0.13       | 0.05 ± 0.23            | 5  | 1.67           |
| 10         | 0.02 ± 0.08 | -0.11 ± 0.06                      | -                               | -               | -                               | -               | -               | -                 | -               | 0.05 ± 0.05                | -                        | -           | -                         | -              | 0.02 ± 0.15       | 0.06 ± 0.24            | 5  | 1.73           |
| 11         | 0.02 ± 0.08 | -0.11 ± 0.06                      | -                               | -               | -                               | -               | -               | -                 | -               | -                          | -                        | -           | -0.05 ± 0.06              | -              | 0.02 ± 0.15       | 0.06 ± 0.25            | 5  | 1.77           |
| 12         | 0.02 ± 0.08 | -0.11 ± 0.06                      | -0.07 ± 0.06                    | -               | -                               | -               | -               | -                 | -               | -0.06 ± 0.06               | -                        | -           | -                         | -              | 0.02 ± 0.14       | 0.06 ± 0.24            | 6  | 1.92           |
| 25         | 0.01 ± 0.08 | -                                 | -                               | -               | -                               | -               | -               | -                 | -               | -                          | -                        | -           | -                         | -              | 0.02 ± 0.16       | 0.06 ± 0.24            | 3  | 2.45           |
| 48         | 0.01 ± 0.08 | -                                 | -0.07 ± 0.06                    | -               | -                               | -               | -               | -                 | -               | -                          | -                        | -           | -                         | -              | 0.02 ± 0.15       | 0.05 ± 0.23            | 4  | 3.18           |
| Full model | 0.02 ± 0.07 | -                                 | -                               | -               | -0.12 ± 0.06                    | -               | -0.18 ± 0.12    | 0.06 ± 0.09       | -               | -                          | -                        | 0.01 ± 0.06 | -0.06 ± 0.06              | 0.12 ± 0.10    | 0.01 ± 0.11       | 0.06 ± 0.25            | 9  | 7.25           |

<sup>a</sup>Reference category is experienced breeder

ratio could be explained by lay date, breeding experience or among good and poor years, with the best supported model only including the helper presence predictor (Table 2, model 1).

Including group composition as a predictor was not supported by the data (Fig. 3, Table 3, model 29 vs. model 24,  $\Delta\text{AICc} = +0.71$ ), suggesting there was no evidence for the local resource competition hypothesis. However, disentangling the facultative within-female from the persistent between-female response showed that these effects were in opposite directions (Fig. 3, Table 3, model 3), with evidence for a persistent ( $\beta = 0.16 \pm 0.07$  SE), but not a facultative response ( $\beta = -0.08 \pm 0.06$  SE; adding the within-female predictor to the best supported model increased AICc values: Table 3, model 3 vs. model 1). These results indicate that those breeding females with relatively more same-sex helpers were also more likely to produce offspring of the overabundant sex (solid red trendline in Fig. 3). This persistent bias was strongly supported by the data, because the between-female predictor was consistently included in the top 61 models and received 0.85 model weight (Table S2). Results also showed some evidence that more experienced females in groups were



**Fig. 3** The mean ( $\pm$ SE) proportion of sons in *M. elegans* broods in relation to group composition (no. of helper males – no. of helper females provisioning the brood) for breeding females living in groups. The solid red trendline represents the significant between-female effect of the ‘group composition’ predictor according to the top model in Table 3, and the dashed blue trendline represents the non-significant within-female effect of the ‘group composition’ predictor according to model 3 in Table 3. The grey dashed line indicates 50/50 offspring sex ratio and the numbers in the bottom represent the number of broods

more likely to produce daughters, although the 95% CI just overlapped zero (Table 3, model 1 vs. model 8).

In contrast to our prediction (Table 1, prediction 2b), the persistent offspring sex ratio bias with respect to group composition was not stronger in female-biased groups compared to male-biased groups. In fact, comparing the slopes (Fig. 1: a vs. b) showed that the bias in offspring sex ratio production was stronger for groups with relatively more male helpers (female-biased groups:  $\beta = 0.001 \pm 0.12$  SE, male-biased groups:  $\beta = 0.15 \pm 0.07$  SE).

Similarly, at the population level, there was no evidence that females persistently biased their offspring sex ratio towards the rarer sex, or that this effect was particularly pronounced with large numbers of females in the population (Table 1, prediction 2c), as including the number of adult (fe)males present in the population increased AICc values (Table S1, model 8 and model 21 vs. model 1).

### Fisher’s hypothesis

In contrast to our prediction under Fisher’s hypothesis (Table 1, prediction 3), at the population level, there was no persistent sex ratio bias towards smaller (i.e. cheaper) female offspring. In fact, offspring sex ratio was slightly biased towards sons (51%), although this was not significantly different from parity (binomial test, proportion of sons, 95% CI [0.49 – 0.52],  $n = 3815$ ,  $P = 0.38$ ).

### Discussion

Females are expected to produce biased offspring sex ratios when fitness returns differ between the sexes, which is hypothesized to depend on the prevailing conditions, like the social environment in cooperatively breeders. However, most studies investigated variation in offspring sex ratios in relation to environmental predictors across females, and although results are often claimed to represent facultative responses, these may as well represent consistent differences among females or environmental conditions directly (e.g. Clutton-Brock et al. 1984; Kruuk et al. 1999). Investigating offspring sex-ratio variation within females across varying conditions provides a powerful method to disentangle these mechanisms (Oddie and Reim 2002). Using repeated measurements (range 1 – 13) of the same females over a nine-year period, we separated phenotypically plastic facultative responses from between-individual correlations and found evidence for both facultative and persistent offspring sex ratio biases in relation to the social environment in cooperatively breeding *M. elegans*.

**Table 3** Summary of model selection results investigating the association between group composition (no. of helper males – no. of helper females) and offspring sex ratio in *M. elegans* broods (n = 493). Predictors were included by their main effect and by using within-subject centring, allowing to distinguish between facultative within-female (within) and persistent between-female (betw) effects. Shown are standardized coefficients (z-scores) with their standard errors (SE). Predictors in the top model of which 95% CI do not overlap zero are shown in bold. Predictor variables that were not fitted in a model are indicated by “–”. Breeding exp: breeding experience of breeding female. See Table S2 for complete model output (50 models)

| Model      | Intercept    | Group composition <sub>within</sub> | Group composition <sub>betw</sub> | Group composition | Lay date <sub>within</sub> | Lay date <sub>betw</sub> | Lay date | Breeding exp <sup>a</sup> | $\sigma^2_{year}$ | $\sigma^2_{female ID}$ | df | $\Delta AIC_c$ | Weight |
|------------|--------------|-------------------------------------|-----------------------------------|-------------------|----------------------------|--------------------------|----------|---------------------------|-------------------|------------------------|----|----------------|--------|
| 1          | -0.06 ± 0.07 | –                                   | <b>0.16 ± 0.07</b>                | –                 | –                          | –                        | –        | -0.12 ± 0.07              | 0.01 ± 0.09       | 0.03 ± 0.17            | 5  | 0.00           | 0.085  |
| 2          | -0.06 ± 0.07 | –                                   | 0.17 ± 0.07                       | –                 | –                          | -0.09 ± 0.07             | –        | -0.12 ± 0.07              | 0.01 ± 0.09       | 0.03 ± 0.17            | 6  | 0.24           | 0.075  |
| 3          | -0.06 ± 0.07 | -0.08 ± 0.06                        | 0.16 ± 0.07                       | –                 | –                          | –                        | –        | -0.11 ± 0.07              | 0.01 ± 0.08       | 0.03 ± 0.17            | 6  | 0.25           | 0.075  |
| 4          | -0.07 ± 0.07 | -0.08 ± 0.06                        | 0.18 ± 0.07                       | –                 | –                          | -0.09 ± 0.07             | –        | -0.10 ± 0.07              | 0.01 ± 0.09       | 0.03 ± 0.18            | 7  | 0.47           | 0.067  |
| 5          | -0.06 ± 0.07 | -0.10 ± 0.06                        | 0.16 ± 0.07                       | –                 | –                          | -0.10 ± 0.06             | –        | –                         | 0.01 ± 0.09       | 0.03 ± 0.17            | 6  | 0.99           | 0.052  |
| 6          | -0.06 ± 0.07 | -0.09 ± 0.06                        | 0.16 ± 0.07                       | –                 | 0.07 ± 0.06                | –                        | –        | -0.12 ± 0.07              | 0.01 ± 0.08       | 0.03 ± 0.17            | 7  | 1.10           | 0.049  |
| 7          | -0.06 ± 0.07 | –                                   | 0.16 ± 0.07                       | –                 | 0.06 ± 0.06                | –                        | –        | -0.13 ± 0.07              | 0.01 ± 0.08       | 0.03 ± 0.17            | 6  | 1.15           | 0.048  |
| 8          | -0.06 ± 0.07 | -0.10 ± 0.06                        | 0.15 ± 0.06                       | –                 | –                          | –                        | –        | –                         | 0.01 ± 0.07       | 0.03 ± 0.16            | 5  | 1.21           | 0.046  |
| 9          | -0.06 ± 0.07 | –                                   | 0.16 ± 0.07                       | –                 | –                          | -0.10 ± 0.06             | –        | –                         | 0.01 ± 0.08       | 0.03 ± 0.16            | 5  | 1.37           | 0.043  |
| 10         | -0.06 ± 0.07 | -0.09 ± 0.06                        | 0.18 ± 0.07                       | –                 | 0.07 ± 0.06                | -0.09 ± 0.06             | –        | -0.11 ± 0.07              | 0.01 ± 0.08       | 0.03 ± 0.18            | 8  | 1.40           | 0.042  |
| 11         | -0.06 ± 0.07 | –                                   | 0.17 ± 0.07                       | –                 | 0.06 ± 0.06                | -0.09 ± 0.07             | –        | -0.12 ± 0.07              | 0.01 ± 0.08       | 0.03 ± 0.17            | 7  | 1.46           | 0.041  |
| 12         | -0.06 ± 0.07 | –                                   | 0.14 ± 0.06                       | –                 | –                          | –                        | –        | –                         | 0.01 ± 0.08       | 0.02 ± 0.15            | 4  | 1.62           | 0.038  |
| 24         | -0.06 ± 0.07 | –                                   | –                                 | –                 | –                          | –                        | –        | –                         | 0.003 ± 0.06      | 0.05 ± 0.23            | 3  | 4.47           | 0.009  |
| 29         | -0.06 ± 0.07 | –                                   | –                                 | 0.06 ± 0.07       | –                          | –                        | –        | -0.11 ± 0.07              | 0.01 ± 0.07       | 0.05 ± 0.22            | 5  | 5.18           | 0.006  |
| Full model | -0.06 ± 0.07 | –                                   | –                                 | 0.05 ± 0.07       | –                          | 0.02 ± 0.06              | –        | -0.12 ± 0.07              | 0.01 ± 0.07       | 0.05 ± 0.22            | 6  | 7.12           | 0.002  |

<sup>a</sup>Reference category is experienced breeder

In the absence of helpers, i.e. when help is most needed, female *M. elegans* did not facultatively bias offspring sex ratio towards daughters; thus, our study does not provide support for the local resource enhancement hypothesis. We predicted such a pattern since offspring have been shown to receive more food and grow faster in the presence of female helpers due to the absence of load-lightening with increasing number of female helpers in the group (Brouwer et al. 2014; MacLeod and Brouwer 2018). Across cooperative breeders, the extent to which offspring sex ratio is biased towards the helpful sex depends on the benefit that helpers provide their parents, with stronger sex ratio adjustments expected when helpers provide more benefits (Griffin and West 2003; Griffin et al. 2005). Support for local resource enhancement has been shown in red-cockaded woodpeckers (*Leuconotopicus borealis*, Gowaty and Lennartz 1985), Seychelles warblers (*Acrocephalus sechellensis*, Komdeur et al. 1997), Alpine marmots (*Marmota marmota*, Allainé et al. 2000), bell miners (*Manorina melanophrys*, Ewen et al. 2003) and western bluebirds (*Sialia mexicana*, Dickinson 2004). Interestingly, these are all species where only one sex regularly helps, and any potential benefit of producing the helping sex is thus relatively large compared to producing the dispersing sex. In contrast, despite the difference in provisioning behaviour between male- and female-biased groups in *M. elegans*, offspring of both sexes do usually stay and help their parents for at least one year (Rowley et al. 1988; Brouwer et al. 2020). Thus, the difference in helper benefits between the sexes is relatively small and this may mean that selection is too weak to drive the evolution of facultative offspring sex ratio adjustment towards females. A similar argument has been used to explain the absence of an overall trend across cooperative breeding bird species (Khwaja et al. 2017). Surprisingly, we found that in the absence of help, females facultatively biased offspring sex ratio towards sons. Although the presence of female helpers is more beneficial for offspring, daughters disperse on average at a younger age compared to sons (annual recruitment probability to breeding position after first year of life: females = 0.48, males = 0.27, Brouwer et al. 2020). Thus, rather than overproducing female offspring, which might only provide help for a single or maybe two seasons, producing male-biased offspring can potentially provide breeders with a workforce for several seasons. Future work will have to quantify the difference in benefits that male and female helpers may provide. Such quantification does not only involve integration of multiple fitness components, but also consideration of the indirect fitness benefits (Brouwer et al. 2020).

In contrast to the prediction under the local competition hypothesis, females living in groups did not facultatively produce a surplus of the sex opposite to the sex of helpers already present. We predicted such a bias in *M. elegans*, because this would increase offspring's future potential, as

dominance status correlates with age whereby every additional same-sex helper is less likely to fill a vacancy (Russell and Rowley 2000). Such density-dependent competition among philopatric offspring has been observed in superb fairy-wrens (*M. cyaneus*) where only sons are philopatric, and where females with three or more male helpers in one year had fewer sons in the next year (Cockburn et al. 2003), and in red-backed fairy-wrens (*M. melanocephalus*), where females biased towards earlier dispersing daughters when helpers were already present and more common at the population level (Varian-Ramos et al. 2010). Despite the absence of a facultative response in relation to the social environment in *M. elegans*, we did find evidence for a persistent offspring sex-ratio bias towards the already overabundant sex of helpers present in the group, and we argue that this among-female effect could have been predicted too.

In cooperative breeders, where helpers are offspring from previous nests that delay dispersal to help rear the next brood, difficulties arise when testing whether helper presence enhances the productivity of the breeding pair, because group size itself will directly depend on reproductive success of the previous year (Cockburn 1998; van de Pol and Brouwer 2021). We propose that a similar problem can arise when analysing offspring sex ratios in relation to the sex of the helpers in the group, when helpers are typically offspring from previous year's broods. Females with a biased offspring sex ratio will be more likely to have helpers of that sex in the next season, and cross-sectional analyses will show a positive correlation between offspring sex ratio and helper sex. This means that rather than evidence for the facultative local resource enhancement hypothesis, such cross-sectional associations might actually provide evidence for environmental driven variation in offspring sex ratio. The persistent offspring sex ratio bias in *M. elegans* could result from consistent among-female differences in body condition or phenotypic traits correlated to sex ratio such as maternally transmitted hormones (Uller et al. 2006; Merklings et al. 2018; Firman 2020). The persistent bias could also be driven by environmental variables directly. For example, in mount-breeding Australian brush-turkeys (*Alectura lathami*), higher and lower than average incubation temperature resulted in sex-biased mortality of embryos (Göth and Booth 2005). However, such a mechanism is unlikely to explain our results, since our observations are close to primary sex ratio.

To conclude, our study shows some evidence for a facultative response with females without helpers producing slower dispersing males. Further, when helpers are typically offspring from previous years broods, cross-sectional analyses are likely to show evidence for persistent rather than facultative offspring sex-ratio biases in relation to the social environment. This could potentially explain previous findings, emphasizing the need for a within-female approach to fully understand the adaptiveness of sex ratio biases.

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**Data availability** The dataset generated during the current study is available as supplementary material.

## Declarations

**Ethics approval** The Australian National University Animal Experimentation Committee licensed our field research and the Western Australian Department of Biodiversity Conservation and Attractions gave permission for fieldwork and sampling (protocol no. A2011/48). Banding was performed with permission of the Australian Bird and Bat Banding Scheme. All applicable international, national and institutional guidelines for the use of animals were followed.

**Conflict of interest** The authors declare no competing interests.

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