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Article

Title: Sex allocation patterns across cooperatively breeding birds do not support predictions of the repayment hypothesis

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Abstract

The repayment hypothesis predicts that reproductive females in cooperative breeding systems overproduce the helping sex. Thanks to well-documented examples of this predicted sex ratio bias, repayment has been considered an important driver of variation in sex allocation patterns. Here we test this hypothesis using data on population brood sex ratios and facultative sex allocation from 28 cooperatively breeding bird species. We find that biased sex ratios of helpers do not correlate with production biases in brood sex ratios, contrary to predictions. We also test whether females facultatively produce the helping sex in response to a deficiency of help (i.e. when they have fewer, or no helpers). Although this is observed in a few species, it is not a significant trend overall, with a mean effect size close to zero. We conclude that, surprisingly, repayment does not appear to be a widespread influence on sex ratios in cooperatively breeding birds. We discuss possible explanations for our results, and encourage further examination of the repayment model.

Introduction

Fisher (1930) formulated an elegant explanation for why sex ratios are so often equal in nature. Because each offspring has a mother and father, any sex that becomes rarer immediately enjoys a reproductive success advantage, and the associated selection pressure drives population sex ratios towards parity. Exceptions to the general rule of equal sex ratios have fascinated evolutionary biologists since (West, 2009). In these cases, producing one sex confers a cost or benefit that trades off against the benefit of rarity underlying Fisher's principle (Hamilton, 1967). Sex allocation by breeders can be viewed as an adaptive decision in the context of parental investment, with the relative costs and benefits of producing each sex being key to its outcome.

In cooperative breeders, one benefit that has attracted a great deal of attention is the fitness gain that parents receive from offspring who help them in future breeding attempts (Malcolm and Marten, 1982; Koenig and Walters, 1999; Griffin et al., 2005). Help is usually more likely to come from one sex than the other (Komdeur, 2004). The 'repayment hypothesis' predicts that parents should invest more in this helpful sex, because of the greater chance that their investment will be repaid through future help (Emlen et al., 1986; Lessells and Avery, 1987). The hypothesis rests on the assumption that apparent help provides a genuine fitness benefit to breeders, and so its predictions only apply where this is the case (see Methods).

The repayment hypothesis yields intuitive predictions about offspring sex ratios in cooperative breeders, and long-term studies of bird populations provide valuable datasets on which to test these. The first general prediction is that offspring sex ratios should be biased towards the helping sex at the population level, because of the extra payoff associated with producing this sex. Brood sex ratios in bell miners (Manorina melanophrys) are consistent with this prediction: helping is extremely male-biased, and 58% of hatchlings are male (Clarke et al., 2002). The second prediction is that breeders with no, or fewer helpers, should facultatively adjust the sex ratio of their broods to be more biased towards the helping sex, as they have more to gain from doing so. Again there is some empirical support, especially from Seychelles warblers (Acrocephalus sechellensis): helping is female-biased in this species, and breeders without helpers produce more females when their territory is of sufficient quality to support the extra philopatric offspring (Komdeur et al., 1997).

Despite these examples, the status of repayment as a widespread driver of sex ratio skew is called into question by a number of negative results. For example, in purple-crowned fairy-wrens (Malurus coronatus) and white-banded tanagers (Neothraupis fasciata), there is no significant bias toward production of the helping sex at the population level, and no evidence for facultative adjustment of brood sex ratios in response to any cues (Kingma et al., 2011; Gressler et al., 2014). While the predictions of the repayment hypothesis are intuitively appealing, the adaptive value of producing each sex will also depend on difficult-to-measure components of the direct fitness of both parents and offspring. Long-term data on red-cockaded woodpeckers (Picoides borealis) have been used to estimate direct fitness differentials between the sexes, and incorporate them into a repayment model; however, the model still failed to predict brood sex ratios at the population level (Koenig and Walters, 1999). A meta-analysis by Griffin et al. (2005) suggests that individuals are more likely to adjust their offspring's sex ratio in systems where the benefits of help are high. This provides some explanation for failures to observe adjustment, but such negative results have proliferated since Griffin et al.'s (2005) study, perhaps because authors realise they run counter to the prevailing view of adaptive sex allocation (Cockburn and Double, 2008).

Here we use a comparative analysis and meta-analysis to test the key predictions of the repayment hypothesis, using data from previously published studies of 28 cooperatively breeding bird species spanning 18 families. We then discuss the usefulness and generality of the concept of repayment, in light of our results.

Methods

We collected data from relevant studies identified using the search term '(brood) sex ratio birds' in Web of Science and Google Scholar, as well as from Koenig and Dickinson (2016), Komdeur (2004) and references within. We also searched the primary literature using Web of Science for any species identified as a kin-based cooperative breeder by Riehl (2013). We only included data from bird species with kin-based cooperative breeding systems, as production is related to future help only in these cases. Where multiple studies were published for the same species, we chose that with the largest sample size, or in the case of Seychelles warblers, that which came from a natural population (Komdeur et al., 1997). Helper sex ratios were obtained from Green et al. (2016) or directly from the literature, where possible from the same population as brood sex ratios. Data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.9bk88 (Khwaja et al., 2017).

Breeding females are only expected to benefit from biasing their offspring's sex ratios towards the helping sex if the help actually improves their fitness in turn (Emlen et al., 1986; Griffin et al., 2005). For this reason, from a dataset of 32 candidate species, we excluded four for which research suggests no positive effect of help on the fitness of breeding females (Table A1). We included a further 10 species in which this effect has not been tested, because help had a positive effect on breeder fitness in 82% of tested species (n = 22). We checked the influence of including these untested species by carrying out a restricted analysis in which they were removed from the dataset.

We investigated the effect of helper sex ratio on log-transformed brood sex ratio across 28 species in the full dataset and 18 species in the restricted dataset, controlling for phylogeny using a phylogenetic generalised least squares (PGLS) model implemented in R 3.2.2 (R Development Core Team, Vienna). We applied this model across 1,000 trees downloaded from birdtree.org (Jetz et al., 2012) using the Hackett et al. (2008) backbone (Fig. 1). Following Green et al. (2016), we included data quality as a variance component in the model, using categories of weak, medium or strong assigned to each study. When assigning these scores, we considered the sample size, length of study, sample size of helper sex ratio estimate and point at which brood sex ratio was measured (with closer to primary sex ratio being considered better quality).

For 16 studies that tested for facultative sex allocation in cooperatively breeding bird species, we used a meta-analysis to investigate the hypothesis that breeders without helpers, or with fewer helpers, show greater production of the helping sex. This is the strongest prediction made by the repayment hypothesis in the context of facultative allocation. We did not include studies of two species for which research suggests no positive effect of help on the fitness of breeding females, for the reasons given above. We extracted effect sizes of the relationship using equations from Lajeunesse (2013), except for two studies where we obtained effect sizes from Griffin et al. (2005). Brood sex ratio was treated as the response, and the predictor was either whether a nest was helped (categorical, 7 studies), or number of helpers (integer, 9 studies). We derived confidence intervals (CI) and sample weights for each study using equations from Lipsey and Wilson (2001), and calculated a weighted mean and 95% CI using the Hmisc package in R (Harrell, 2016).

Results

We included data on helper and brood sex ratios for 28 species of cooperatively breeding bird. The mean brood sex ratio (proportion of males) across species was 0.52 ± 0.01 SE (median = 0.51); this value ranged from 0.37 in broods of the black-eared miner (Manorina melanotis), to 0.69 in broods of the splendid fairy-wren (Malurus splendens). The mean helper sex ratio across species was 0.80 ± 0.05 SE (median = 0.89), ranging from 0.10 in white-throated magpie-jays (Calocitta formosa), to exclusively male helpers in 10 species (Table A2).

There was effectively no phylogenetic signal to brood sex ratio (PGLS: $\lambda < 0.01$; Fig. 1). As expected, studies with a data quality score of weak accounted for more variance ($1.23\lambda \times 10^9$) than those scoring medium ($2.41\lambda \times 10^8$), and those scoring strong accounted for the least ($1.30\lambda \times 10^7$). Once these effects were controlled, we found no relationship between brood sex ratio and helper sex ratio (PGLS: effect of helper sex ratio = 0.04 ± 0.06 SE, $R^2 < 0.01$, $t = 0.67$, $P = 0.509$; Fig. 2). With phylogeny accounting for such little variation, a simple linear model without phylogenetic or data quality controls produced equivalent results (ANOVA: effect of helper sex ratio = 0.02 ± 0.09 SE, $R^2 < 0.01$, $F_{1, 26} = 0.03$, $P = 0.857$). Removing the 10 species for which benefits of help to breeders were unconfirmed also produced equivalent results (PGLS: effect of helper sex ratio = 0.04 ± 0.06 SE, $R^2 = 0.08$, t = 0.67, P = 0.515).

We obtained effect sizes of the relationship between number of helpers or being helped, and brood sex ratios, from studies of 16 cooperatively breeding bird species (Fig. 3; Table A3). Seven of these effects were in the expected direction, with more of the helping sex produced by unhelped females or those with fewer helpers. Seven were in the opposite direction, and the directions of two small effects were not reported. The weighted mean of the 14 effect sizes whose direction was reported was 0.01 (95% CI = -0.17-0.36) in the direction expected. This result was the same (to two decimal places) when both excluded effect sizes were treated as positive and the weighted mean shifted to 0.00 when they were treated as negative. Effect sizes have been closer to zero in more recent studies (ANOVA: effect of year = -0.01, $R^2 = 0.50$, $F_{1, 14} = 14.24$, P = 0.002; Fig. 4), notably since the publication of Griffin et al.'s (2005) meta-analysis of sex ratio adjustment in cooperative breeders.

Discussion

We investigated two general predictions attributed to the repayment hypothesis. The first is that in kin-based cooperative breeders, females produce broods biased towards the helpful sex, because the future fitness contribution made by helpers repays some of their investment. Across 28 bird species, we found no evidence that this was generally the case, despite a lack of phylogenetic signal indicating that brood sex ratio is a labile trait. The second prediction was that females in need of help adjust their brood’s sex ratios further in favour of the helping sex. We drew together tests of this prediction from 16 studies, and although it is borne out in a minority of cases, there was not a significant directional trend across species. Earlier studies reported greater effect sizes than more recent studies, which may have led to an overestimation of the prevalence of adaptive sex allocation in the literature.

No overall bias towards producing the more helpful sex

A predicted global sex-ratio skew toward the helping sex in cooperative breeders is the most direct interpretation of the repayment model; in their introduction to the original model, Emlen et al. (1986) proposed that ‘the sex ratio should achieve an equilibrium in which there is an overproduction of the helper sex’. There are two levels at which this prediction may falter: proper accounting of the costs and benefits of producing each sex, and empirical observation. Where sexes differ in their tendency to help, they are also likely to differ in other key life-history traits. Although one sex may ‘repay’ investment by helping and thus improving their parents’ productivity, this could feasibly be counteracted by enhanced reproductive success in the non-helping sex improving parents’ production of grand-offspring. If this is the case, biased brood sex ratios should not be adaptive. This important point was identified by Koenig and Walters (1999), who incorporated sex differences in survival and reproductive success into an extended repayment model that aimed to predict optimal brood sex ratios in red-cockaded woodpeckers. Their results were interesting in two respects: (1) the predicted optimal brood sex ratio in this species with male-biased help was still male-biased, and was little affected by considering differences in the direct fitness achieved by male and female offspring, and (2) the predicted optimal brood sex ratio was significantly different from observed sex ratios, which were close to parity. Here, we were unable to account for the relative influence of offspring and grand-offspring production on expected sex ratios, because very few species in our sample have been studied in as much detail as the red-cockaded woodpecker. Instead, we used helper sex ratio, the key driver of expected brood sex ratio bias in Koenig and Walters (1999), and similarly found that observed brood sex ratios do not fit expectation. This does not necessarily mean that the extended repayment model as applied to red-cockaded woodpeckers also fails in other systems; it is still possible that this species is exceptional, and that in most cases including sex differences in future productivity may better explain observed patterns (but see Koenig et al., 2001). For example, the benefits of rarity identified by Fisher (1930) may be much greater than the marginal fitness benefits associated with likelihood of helping. Nevertheless, in general, our results suggest that females biasing production towards the helping sex, which is the most intuitive prediction of repayment models, is not a valid generalisation.

The repayment hypothesis makes opposite predictions to the local resource competition hypothesis, which suggests that females may benefit from overproducing the dispersive (generally non-helping) sex, to reduce competition for resources (Clark, 1978). Costs of competition could explain the discrepancy between our predictions and results, though there are reasons to doubt this interpretation. Firstly, in most systems the benefits of help appear to compensate for any costs because helped nests are usually provisioned more frequently (Hatchwell, 1999) and are generally more productive (Dickinson and Hatchwell, 2004; Koenig and Dickinson, 2016). Furthermore, if competition provided the main constraint to adaptively biasing the sex ratio, we would expect biases towards the helping sex to be especially pronounced in species like riflemen (*Acanthisitta chloris*), where most helpers had previously dispersed from their natal territory and the sexes do not differ significantly in their dispersal distances (Preston, 2012). It is noteworthy, therefore, that the observed sex ratio is close to parity in this species (Khwaja, 2017). Nevertheless, competition may limit the adaptive value of biased sex allocation in other species.

A third possible explanation is simply that biasing brood sex ratios is constrained or costly, though again this has little support. Mechanisms of biased sex allocation are currently unknown, and some suggestions rely on potentially taxon-specific characteristics such as size dimorphism in the centromeres of sex chromosomes (Rutkowska and Badyaev, 2008). However, our models showed a complete lack of phylogenetic constraint on brood sex ratios. Although across species these average around parity, some studies with convincingly large sample sizes show significantly biased population brood sex ratios (Clarke et al., 2002; Cockburn and Double, 2008). There may be a mechanistic barrier to biasing sex ratios in some species, but as this is clearly not global, and phylogenetically random, it is not a well-supported interpretation (West and Sheldon, 2002). While a combination of the three explanations we have suggested may underlie our results, none are especially convincing for the reasons discussed. We would welcome a theoretical re-evaluation of the repayment model, which may make sense of its uneasy fit with empirical data.

Rarity of facultative production of the more helpful sex

A final candidate explanation for this lack of population-level brood sex ratio biases is that biases may be context-dependent rather than consistent (Pen and Weissing, 2000). Females may bias their broods' sex ratios only when they have fewer, or no helpers (for such facultative manipulation, the local resource competition and repayment hypotheses make the same rather than opposite predictions). In contrast to the lack of evidence for population-level sex ratio biases, a few studies do provide strong support for facultative control of sex ratios. In Seychelles warblers, females show extraordinarily sophisticated control of their broods' sex ratios, with females (the more helpful sex) overproduced on good quality territories without existing helpers (Komdeur et al., 1997, 2002). This does not, however, result in an overall population-level bias towards the production of females because males (the more dispersive sex) are overproduced on poor quality territories where supernumeraries are likely to be costly. Thus, in this case, an unbiased population sex ratio is consistent with the repayment hypothesis because females across different contexts adaptively allocate their offspring's sex. Western bluebirds (Sialia mexicana) also show evidence of facultative control (Dickinson, 2004), but in general, our meta-analysis shows that these species are the exception rather than the rule (with an average effect size close to zero). There is no general tendency across species to produce the helping sex when breeders are deficient of help. This picture emerges strongly with the inclusion of more recent publications documenting negative results, providing a contrast to the mainly positive findings published by the time of Griffin et al.'s (2005) previous meta-analysis, and leading us to somewhat different conclusions (Fig. 4). We hope this encourages publication of negative results, which are essential for the validity of comparative work.

Our findings raise the question of why helpers are apparently not facultatively produced in response to ‘need’ in other species, where there may be a plausible benefit to doing so; or what is exceptional about Seychelles warblers? One unusual feature of this species’s breeding system is that although females are more likely to become helpers than males, they are also more likely to become subordinate cobreeders who lay their own egg in the nest of the dominant pair (Richardson et al., 2001, 2002). This provides an additional selection pressure against producing philopatric females on poor-quality territories, as their potential reproduction would place further strain on resources; it is conceivable that without this additional pressure, the benefits of manipulation may not outweigh its costs (see Pen et al., 1999). As well as other species lacking such a dual selective pressure on sex ratio manipulation, we outline four suggestions below that may explain why the helping sex is elsewhere rarely overproduced in response to apparent need.

Unpredictable environments. Adaptive sex allocation in Seychelles warblers relies on assessment of environmental quality. Philopatric females are overproduced only on territories with sufficient food (Komdeur et al., 1997). Cooperatively breeding birds are commonly associated with unpredictable environments, with extra care thought to buffer against stochasticity (Jetz and Rubenstein, 2011; but see Griesser and Suzuki, 2016). Species living in such conditions may lack adaptive cues for sex allocation. In acorn woodpeckers (*Melanerpes formicivorus*), helpers have a generally positive effect on breeders’ reproductive success, but this effect becomes negative when conditions are poor (Koenig et al., 2011). A change in environmental conditions may therefore cancel any adaptive benefit of facultatively producing philopatric males.

Unpredictable help. In species that breed in kin neighbourhoods, such as riflemen and long-tailed tits (Aegithalos caudatus), helpers are not permanently affiliated with the breeding pair (Hatchwell, 2009). Respectively, helpers in these species begin the breeding season dispersed onto their own territories, or attempting to breed themselves, and they start helping at a nest partway through the provisioning phase (Preston et al., 2013; Hatchwell, 2016). As a result, breeding females may not have good information on the amount of help they will receive (Nam et al., 2011). This constraint is not limited to species in kin neighbourhoods: even in cooperative groups formed by delayed dispersal, it is sometimes the case that not all group members help (e.g. Rubenstein, 2016), and therefore group size may be an inaccurate cue for assessing future help. Unpredictable help limits the potential for female breeders to make adaptive sex allocation decisions based on need.

Other cues influencing allocation decisions. Sociable weavers (Philetairus socius) display a surprising sex allocation pattern, in which females with helpers produce relatively more rather than fewer males, the helping sex (Doutrelant et al., 2004). Clearly in this species the need for help is not a key driver of allocation decisions; the authors suggest the inheritance of within-colony rank by philopatric males may select for overproduction of males by high-ranking breeders, which would inevitably correlate with levels of help. In white-winged fairy-wrens (Malurus leucopterus) and superb starlings (Lamprotornis superbus), sex allocation is consistent with the Trivers-Willard hypothesis, where females with better reproductive prospects overproduce males, who have higher potential fitness (Trivers and Willard, 1973; Rathburn and Montgomerie, 2005; Rubenstein, 2007). In these species, allocation decisions based on rank and breeding condition presumably carry more benefit than those based on a need for help.

Insufficient benefits of help. Griffin et al. (2005) found that the benefit of help was key to the extent of facultative production of the helping sex. They used helpers' effect on productivity as a measure of this benefit. There are issues with this approach, as in some species helpers improve downstream recruitment rather than breeding productivity, and in others they have less effect on productivity but provide direct benefits to breeders through load-lightening (Hatchwell, 1999; Hatchwell et al., 2004; Preston et al., 2016). Quantifying the total benefit that help provides to breeders is therefore challenging and potentially misleading. Nevertheless, variation in the true value of this effect is likely to explain some of the wide variation in patterns of sex ratio adjustment that we have identified in this study.

Conclusion

The repayment hypothesis is strongly supported in certain species of cooperatively breeding bird, but our study shows that its predictions do not explain variation across species. On a generalised level, we find that its importance is marginal in driving both sex ratio biases and facultative sex allocation. We have suggested several factors that may confound predicted results, but it is surprising that predictions from such an intuitively appealing theory do not fit observed patterns. This contrasts with the majority of work on sex allocation, in which theoretical predictions have matched empirical results with a great deal of success (West, 2009). We conclude that repayment is an occasional, but not widespread, influence on sex allocation in cooperatively breeding birds.

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Appendix: species selection and data tables

Table A1 Species selection.

Species	**Included**	**Effect of help**	**Reference**
Harris's hawk (Parabuteo unicinctus)	No	NP	Bednarz (1987)
Green woodhoopoe (Phoeniculus purpureus)	No	NP	Du Plessis (1993)
Acorn woodpecker (Melanerpes formicivorus)	F + S	P + LL	Koenig et al. (2011)
Red-cockaded woodpecker (Picoides borealis)	F + S	P + LL	Walters and Garcia (2016)
Laughing kookaburra (Dacelo novaguineae)	F + S	LL	Legge (2000)

Species	**Included**	**Effect of help**	**Reference**
Pied kingfisher (Ceryle rudis)	F + S	P	Reyer (1990)
Monk parakeet (Myiopsitta monachus)	F	?	
Rifleman (Acanthisitta chloris)	F + S	P	Preston et al. (2016)
Bell miner (Manorina melanophrys)	F	?	
Black-eared miner (Manorina melanotis)	F	?	
Noisy miner (Manorina melanocephala)	F	?	
Southern emu-wren (Stipiturus malachurus)	F	?	
Purple-crowned fairy-wren (Malurus coronatus)	F + S	P + LL	Kingma et al. (2010)
White-winged fairy-wren (Malurus leucopterus)	F	?	
Red-backed fairy-wren (Malurus melanocephalus)	No	NP	Varian-Ramos et al. (2010)
Superb fairy-wren (Malurus cyaneus)	F + S	LL	Cockburn et al. (2016)
Splendid fairy-wren (Malurus splendens)	F + S	LL	Russell and Rowley (1988)
Rufous vanga (Schetba rufa)	F + S	LL	Eguchi et al. (2009)
Apostlebird (Struthidea cinerea)	F + S	P	Woxvold and Magrath (2005)
American crow (Corvus brachyrhynchos)	F	?	
Florida scrub-jay (Aphelocoma coerulescens)	F + S	P	Fitzpatrick and Bowman (2016)
White-throated magpie-jay (Calocitta formosa)	F + S	P	Innes and Johnston (1996)
Ground tit (Pseudopodoces humilis)	No	NP	Du and Lu (2009)
Seychelles warbler (Acrocephalus sechellensis)	F + S	P	Komdeur et al. (2016)
Puff-throated babbler (Alophoixus pallidus)	F	?	

Species	**Included**	**Effect of help**	**Reference**
Long-tailed tit (Aegithalos caudatus)	F + S	P + LL	Hatchwell (2016)
Sociable weaver (Philetairus socius)	F + S	P	Covas et al. (2008)
White-banded tanager (Neothraupis fasciata)	F	?	
Palila (Loxioides bailleui)	F	?	
Western bluebird (Sialia mexicana)	F + S	P	Dickinson et al. (2016)
Superb starling (Lamprotornis superbus)	F + S	P	Rubenstein (2007)
Galápagos mockingbird (Mimus parvulus)	F + S	P + LL	Kinnaird and Grant (1981)

Species of kin-based cooperative breeders for which appropriate sex ratio data were available, with justification for inclusion or exclusion from the study. Species in which research suggests helpers do not benefit breeding females were excluded. Species in which this relationship has not been tested were included in the full analysis (F), but excluded from the strict analysis (S). Positive effects of helpers on breeder fitness were either enhancing productivity (P), load-lightening (LL) or both. Otherwise, effects were either not positive (NP) or not tested (?).

Table A2 Sex ratio data used in comparative analysis.

Species	**BSR**	**Source**	**HSR**	**Source**
Acorn woodpecker (Melanerpes formicivorus)	0.48	Koenig et al. (2001)	0.58	Koenig et al. (2016)
Red-cockaded woodpecker (Picoides borealis)	0.50	Koenig and Walters (1999)	0.95	Lennartz et al. (1987)
Pied kingfisher (Ceryle rudis)	0.53	Reyer (1990)	1.00	
Laughing kookaburra (Dacelo	0.47	Legge et al. (2001)	0.76	Legge and

Species	**BSR**	**Source**	**HSR**	**Source**
novaeguineae)				Cockburn (2000)
Monk parakeet (Myiopsitta monachus)	0.46	Eberhard (1998)	0.75	Bucher et al. (2016)
Rifleman (Acanthisitta chloris)	0.47	Khwaja (2017)	0.72	
Bell miner (Manorina melanophrys)	0.56	Clarke et al. (2002)	0.88	Wright et al. (2010)
Black-eared miner (Manorina melanotis)	0.37	Ewen et al. (2001)	0.96	
Noisy miner (Manorina melanocephala)	0.50	Arnold et al. (2001)	0.99	
Southern emu-wren (Stipiturus malachurus)	0.48	Maguire and Mulder (2004)	1.00	
Purple-crowned fairy-wren (Malurus coronatus)	0.53	Kingma et al. (2011)	0.69	Kingma et al. (2009)
White-winged fairy-wren (Malurus leucopterus)	0.50	Rathburn and Montgomerie (2005)	1.00	
Superb fairy-wren (Malurus cyaneus)	0.53	Cockburn and Double (2008)	1.00	
Splendid fairy-wren (Malurus splendens)	0.69	Mulder (1994)	1.00	Webster et al. (2004)
Rufous vanga (Schetba rufa)	0.56	Asai et al. (2003)	1.00	
Apostlebird (Struthidea cinerea)	0.58	Woxvold and Magrath (2008)	0.58	Woxvold et al. (2006)
American crow (Corvus brachyrhynchos)	0.58	Caffrey (1992)	0.39	
Florida scrub-jay (Aphelocoma coerulescens)	0.49	Fitzpatrick and Bowman (2016)	0.54	Woolfenden and Fitzpatrick (1984)
White-throated magpie-jay (Calocitta formosa)	0.50	Berg (2004)	0.10	
Seychelles warbler (Acrocephalus sechellensis)	0.54	Komdeur et al. (1997)	0.37	Richardson et al. (2002)

Species	BSR	Source	HSR	Source
Puff-throated bulbul (Alophoixus pallidus)	0.50	Sankamethawee et al. (2010)	1.00	
Long-tailed tit (Aegithalos caudatus)	0.53	Nam et al. (2011)	0.86	Hatchwell et al. (2004)
Sociable weaver (Philetairus socius)	0.57	Komdeur (2004)	0.80	Covas et al. (2006)
White-banded tanager (Neothraupis fasciata)	0.50	Gressler et al. (2014)	1.00	Manica and Marini (2011)
Palila (Loxioides bailleui)	0.63	Lindsey et al. (1995)	1.00	Patch-Highfill (2008)
Western bluebird (Sialia mexicana)	0.51	Koenig and Dickinson (1996)	1.00	Dickinson et al. (1996)
Superb starling (Lamprotornis superbus)	0.45	Rubenstein (2007)	0.62	
Galápagos mockingbird (Mimus parvulus)	0.51	Curry and Grant (1989)	0.90	Grant (1988)

Brood sex ratio (BSR) and helper sex ratio (HSR), expressed as proportion of males, for 28 cooperatively breeding bird species. Source references are specified for HSR where these differ from the source for BSR.

Table A3 Effect sizes for facultative adjustment used in meta-analysis.

Study	Species	r	Calculated from
Koenig et al. (2001)	Acorn woodpecker (Melanerpes formicivorus)	+0.03	Comparison of proportions[1]
Gowaty and Lennartz (1985)	Red-cockaded woodpecker (Picoides borealis)	+0.36	Obtained from Griffin et al. (2005)[2]
Legge et al. (2001)	Laughing kookaburra (Dacelo novaeguineae)	-0.17	GLMM[1]

Study	**Species**	**r**	**Calculated from**
Khwaja (2017)	Rifleman (Acanthisitta chloris)	-0.08	GLMM[1]
Ewen et al. (2003)	Bell miner (Manorina melanophrys)	+0.08	GLM[2]
Kingma et al. (2011)	Purple-crowned fairy-wren (Malurus coronatus)	+0.02	GLMM[2]
Cockburn and Double (2008)	Superb fairy-wren (Malurus cyaneus)	-0.05	GLMM[2]
Rathburn and Montgomerie (2005)	White-winged fairy-wren (Malurus leucopterus)	+0.05	GLM[2]
Woxvold and Magrath (2008)	Apostlebird (Struthidea cinerea)	?0.06	GLMM[2]
Canestrari et al. (2012)	Carrion crow (Corvus corone)	-0.00	GLMM[2]
Komdeur et al. (1997)	Seychelles warbler (Acrocephalus sechellensis)*	+0.36	G-test[1]
Nam et al. (2011)	Long-tailed tit (Aegithalos caudatus)	-0.05	GLM[1]
Doutrelant et al. (2004)	Sociable weaver (Philetairus socius)	-0.34	GLMM[1]
Gressler et al. (2014)	White-banded tanager (Neothraupis fasciata)	+0.08	GLMM[1]
Dickinson (2004)	Western bluebird (Sialia mexicana)	+0.24	Obtained from Griffin et al. (2005)[2]
Rubenstein (2007)	Superb starling (Lamprotornis superbus)	?0.05	GLM[2]

Effect sizes (r) for the relationship between a female being helped[1] or her number of helpers[2], and her brood’s sex ratio, across 16 cooperatively breeding bird species. Positive effect sizes are in the direction expected from theory: greater production of the helping sex when a female is unhelped or has fewer helpers; ? denotes effect sizes of unknown direction. Species marked * are those where helping is female-biased; it is male-biased in all others.

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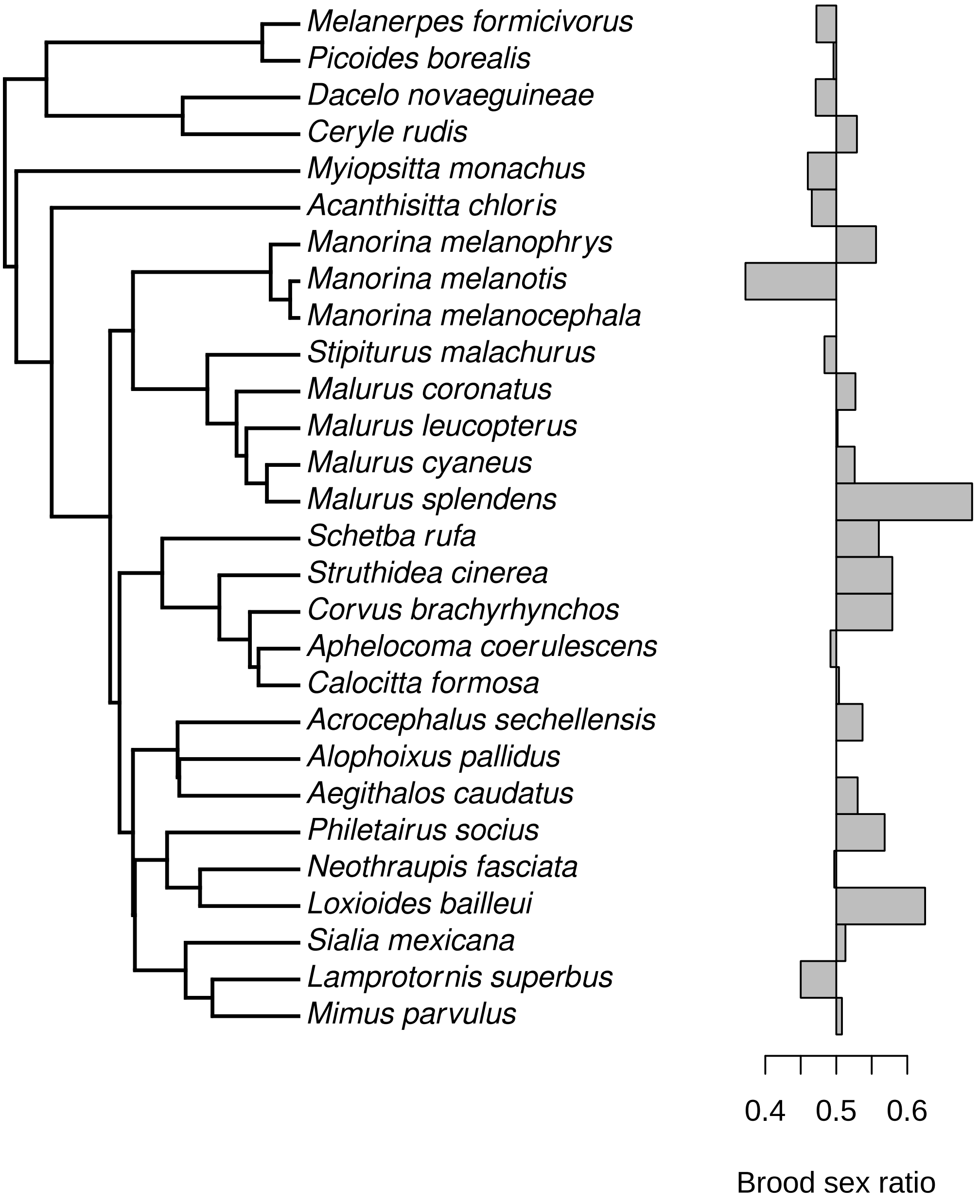
Figure legends

Fig. 1 Phylogeny showing relationships between the 28 species used in our comparative analysis, with branch lengths from 1 of 1,000 sampled trees downloaded from birdtree.org (Jetz et al., 2012). Brood sex ratio for each species is expressed as the mean proportion of males in broods from a studied population. Brood sex ratio is randomly distributed with respect to phylogeny (see Results). M. monachus, M. melanophrys, M. melanotis, M. melanocephala, S. malachurus, M. leucopterus, C. brachyrhynchos, A. pallidus, N. fasciata and L. bailleui were excluded from a restricted analysis because of unconfirmed effects of help on breeder fitness (see Methods).

Fig. 2 Observed sex ratios of helpers and broods across 28 cooperatively breeding bird species, expressed as proportions of males. There is no relationship between these two variables (see Results), in contrast to the predictions of the repayment hypothesis. Point sizes represent our assessment of data quality (large points representing strongest data). Filled points correspond to species where benefits of help to breeders are unconfirmed; these were removed from a restricted analysis (see Methods).

Fig. 3 Effect sizes and confidence intervals from 14 studies investigating facultative production of the more helpful sex in cooperatively breeding birds. Positive effect sizes are in the direction expected from theory: females producing more of the more helpful sex when deficient of help. The effect sizes of two studies (on apostlebirds and superb starlings) are not shown because their directions were not reported (see Results).

Fig. 4 The relationship between the magnitude of effect sizes from studies investigating facultative sex allocation in cooperative breeders, and their year of publication (see Results). The directions of the effects are not shown: this plot represents their distance from zero.


Melanerpes formicivorus
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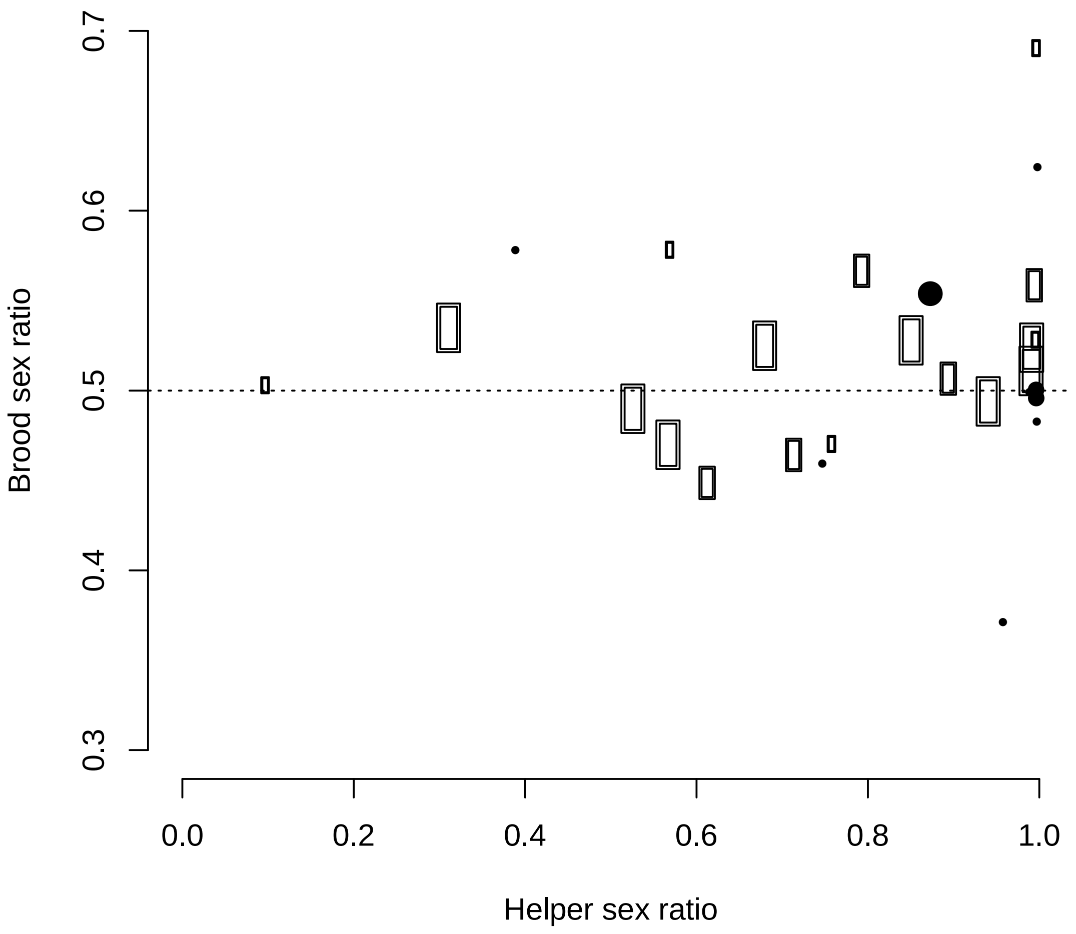
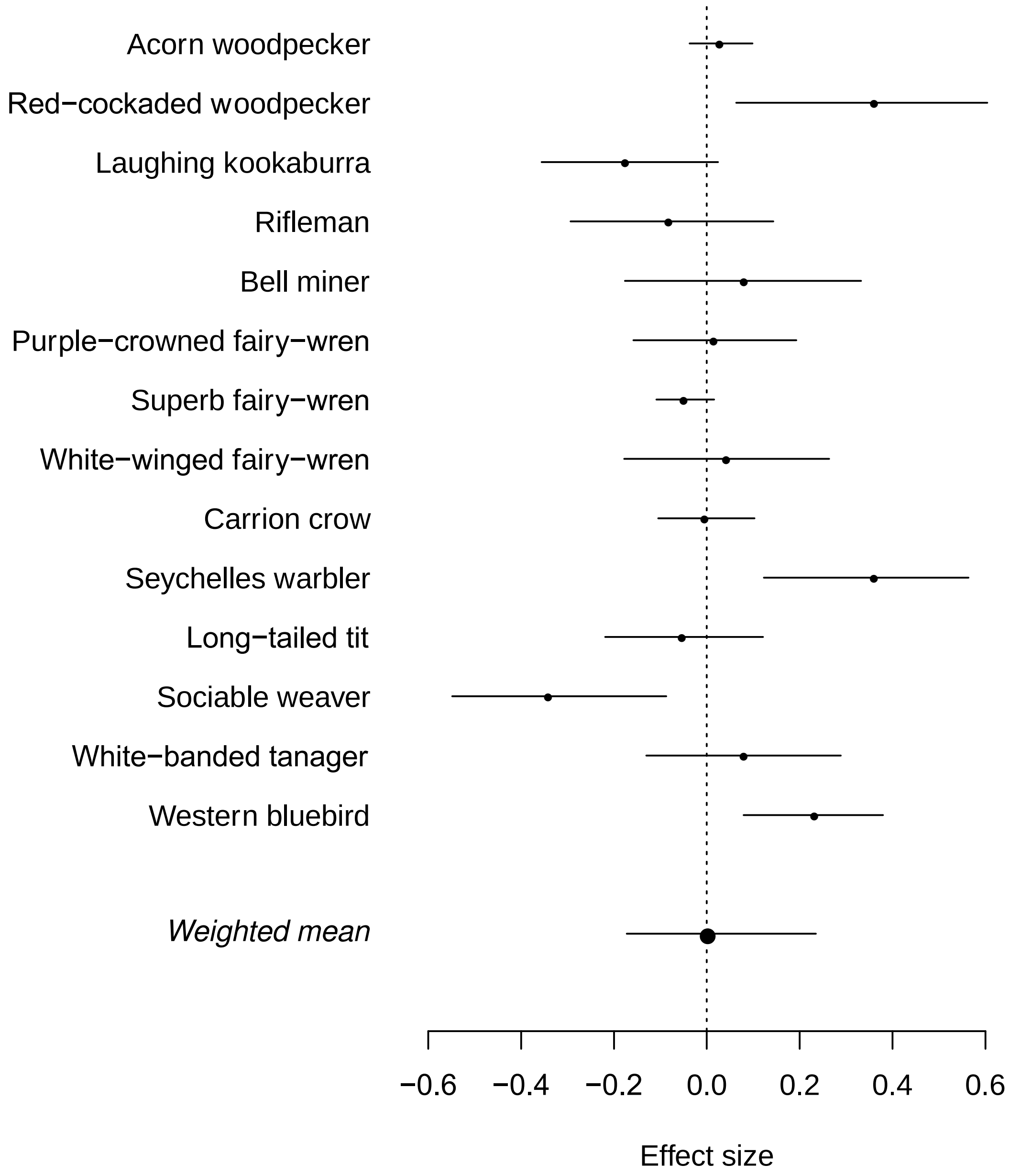
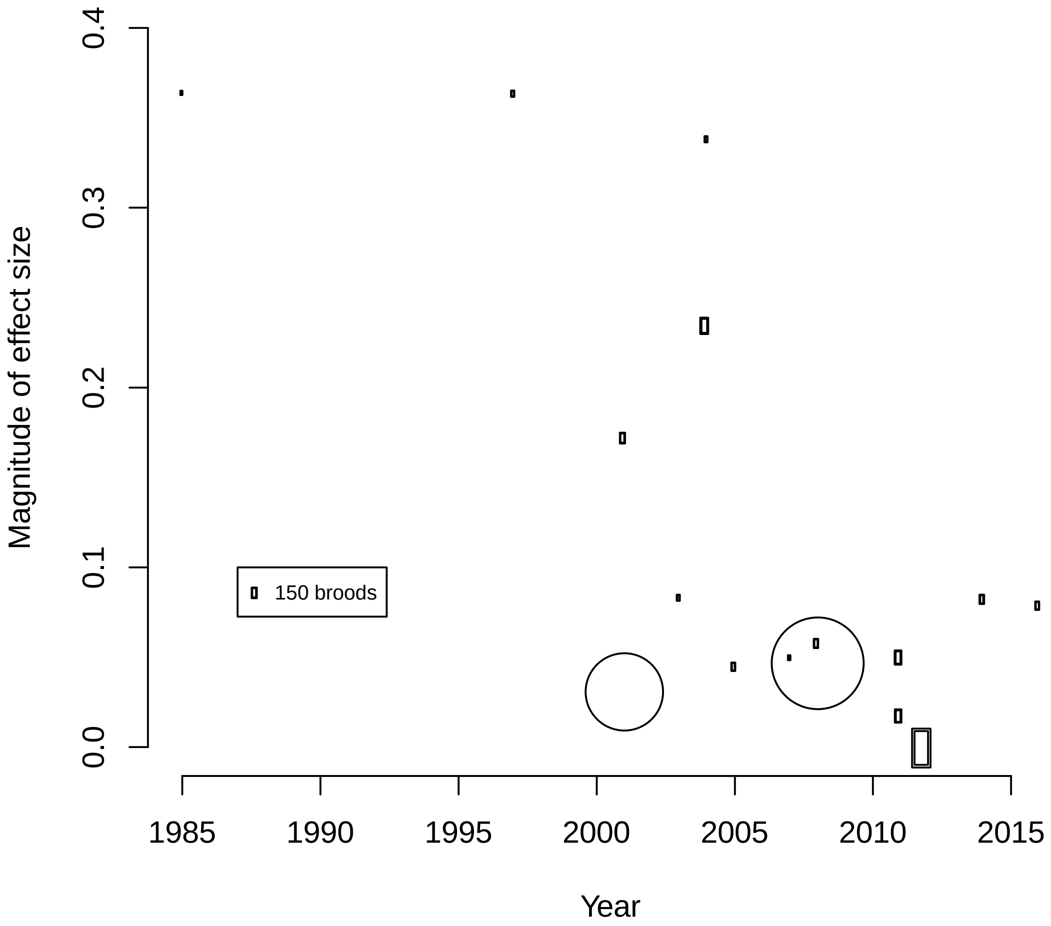
Myiopsitta monachus
Acanthisitta chloris
Manorina melanophrys
Manorina melanotis
Manorina melanocephala
Stipiturus malachurus
Malurus coronatus
Malurus leucopterus
Malurus cyaneus
Malurus splendens
Schetba rufa
Struthidea cinerea
Corvus brachyrhynchos
Aphelocoma coerulescens
Calocitta formosa
Acrocephalus sechellensis
Alophoixus pallidus
Aegithalos caudatus
Philetairus socius
Neothraupis fasciata
Loxioides bailleui
Sialia mexicana
Lamprotornis superbus
Mimus parvulus
0.4
0.5
0.6
Brood sex ratio


0.7
0.6
0.5
0.4
0.3
Brood sex ratio
0.0
0.2
0.4
0.6
0.8
1.0
Helper sex ratio


Acorn woodpecker
Red−cockaded woodpecker
Laughing kookaburra
Rifleman
Bell miner
Purple−crowned fairy−wren
Superb fairy−wren
White−winged fairy−wren
Carrion crow
Seychelles warbler
Long−tailed tit
Sociable weaver
White−banded tanager
Western bluebird
Weighted mean
−0.6
−0.4
−0.2
0.0
0.2
0.4
0.6
Effect size


0.4
0.3
0.2
0.1
0.0
Magnitude of effect size
150 broods
1985
1990
1995
2000
2005
2010
2015
Year