



No evidence for adaptive sex ratio adjustment in a cooperatively breeding bird with helpful helpers

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Abstract

Repayment hypothesis for offspring sex allocation predicts that breeders in cooperatively breeding groups should overproduce the helping sex, particularly when they lack helpers. In birds that produce sexually size-dimorphic nestlings, sex allocation is further predicted to vary across hatching order to maximize brood survival. This could occur by biasing late-hatched nestlings toward either the energetically inexpensive sex (the intra-brood sharing-out hypothesis) or the more competitive sex (the intra-brood competitive equilibrium hypothesis). Here, we test these hypotheses using data from 553 nestlings in 109 broods of greater anis (*Crotophaga major*), a cooperatively breeding bird that breeds in groups composed of multiple reproductive pairs and non-breeding helpers. Helpers are predominantly males and increase the reproductive output of breeders; late-hatched nestlings are more vulnerable to starvation. Therefore, the repayment hypothesis predicts that groups without helpers should produce male-biased broods, whereas the intra-brood sharing-out and competitive equilibrium hypotheses predict that either females (the energetically inexpensive sex) or males (the more competitive sex), respectively, should be overproduced at the end of the laying sequence. Contrary to these predictions, population-wide sex ratios did not differ significantly from 50:50, and we found no evidence for facultative sex ratio adjustment within broods by helper presence or by hatch order. These results support a growing consensus that facultative sex allocation is less widespread in birds than once thought, even in cooperatively breeding species with sex-biased helping behavior.

Significance statement

Evolutionary biologists have long been interested in offspring sex ratios. Despite a rich body of literature, few clear trends have emerged among the many hypotheses proposed to explain offspring sex biases in birds, and relatively few studies have examined multiple hypotheses or long-term datasets. This study leverages an 11-year dataset on the cooperatively breeding greater ani to address three adaptive hypotheses for offspring sex allocation. However, consistent with recent meta-analyses, we find no support for adaptive sex allocation in line with the predictions of any of the three hypotheses. Facultative adjustment of sex ratios in birds may be more constrained than once thought, even in species in which it is predicted to be adaptive.

Keywords Sex allocation · Cooperative breeding · Repayment hypothesis · Birds · Sexual dimorphism · Hatching asynchrony

Introduction

The possibility that animals can adaptively adjust the sex of their offspring at conception has long fascinated theoreticians and field biologists alike. Although sex ratio bias has been hypothesized to be adaptive in many situations, sex ratios in natural populations tend to be balanced (1:1), a phenomenon whose evolutionary significance was first discussed by Darwin (1871) and explored more formally by Düsing (1883, 1884) and Fisher (1930). The Düsing-Fisher model argues that frequency-dependent selection

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favors equal investment in male and female offspring and, thus, that unbiased sex ratios tend to be evolutionarily stable (Queller 2006). Despite this, biologists have documented dramatic exceptions to this general rule, particularly among the Hymenoptera (Trivers and Hare 1976; Herre 1987), and understanding the evolution of these exceptions remains central to sex allocation research (West 2009). Theory predicts that it can be adaptive for a mother to bias the sex of her offspring when (1) current conditions affect the future fitness of male and female offspring differently (Trivers and Willard 1973; Charnov 1982; Leimar 1996) or (2) the direct costs to the mother of producing a son and daughter differ. The latter context can occur when one sex requires more resources to produce (the costly sex hypothesis: Fisher 1930; Patterson et al. 1980; Ligon and Ligon 1990) or, for species that breed cooperatively, when offspring of one sex are more likely to delay dispersal and assist their parents as non-breeding helpers (the repayment hypothesis: Gowaty and Lennartz 1985; Emlen et al. 1986; Komdeur 2004).

Although the most compelling examples of adaptive sex ratio bias have been observed in insects, cooperatively breeding birds have emerged as model systems for empirical tests of adaptive hypotheses in vertebrates, especially the repayment hypothesis. A common criticism of sex ratio research in vertebrates is that studies are often exploratory and lack clear predictions about the direction of bias (Frank 1990; Cockburn et al. 2002; West and Sheldon 2002). Studies of cooperatively breeding birds provide an opportunity to resolve this problem since, in some species, offspring of one sex are more likely to act as helpers. In these species, the intensity of selection on sex ratios should be proportional to the fitness benefit that non-breeding helpers provide their parents and the extent to which helping is sex biased; thus, selective pressures are quantifiable and should vary predictably among species (Gowaty and Lennartz 1985; Pen and Weissing 2000).

This framework initially generated promising results, with several studies finding sex ratio biases in the direction predicted by the repayment hypothesis (e.g., red-cockaded woodpeckers *Picoides borealis*, Gowaty and Lennartz 1985; green woodhoopoes *Phoeniculus purpureus*, Ligon and Ligon 1990; Seychelles warblers *Acrocephalus sechellensis*, Komdeur et al. 1997; bell miners *Manorina melanophrys*, Clarke et al. 2002). An early meta-analysis by Griffin et al. (2005), which included 11 cooperatively breeding species (9 birds and 2 mammals), found that the degree of bias was positively correlated with the magnitude of fitness benefits provided by helpers. This suggested that adaptive sex allocation was widespread in cooperative breeders and that variation in bias was largely explained by variation in the benefits of help. In subsequent years, however, some studies failed to demonstrate biased sex ratios, even in cooperatively breeding species with well-documented benefits of helping (e.g.,

white-throated magpie-jays *Calocitta formosa*, Berg 2004; superb fairywrens *Malurus cyaneus*, Cockburn and Double 2008; long-tailed tits *Aegithalos caudatus*, Nam et al. 2011). A larger meta-analysis by Khwaja et al. (2017), which included 28 bird species in which helpers increase breeder fitness, found that population-level sex ratios were not systematically biased toward the helping sex and that females did not generally overproduce the helping sex when they lacked help. Unbiased sex ratios were at least as common as biased sex ratios, and the average effect size of helper presence on offspring sex was close to zero. Khwaja et al. (2017) also noted that the proportion of studies reporting unbiased sex ratios had increased over time, suggesting an earlier publication bias against negative results (see also Cockburn and Double 2008). Therefore, more empirical studies are needed to determine whether the predictions of the repayment hypothesis are broadly supported across cooperative breeders.

In this study, we test adaptive hypotheses for sex ratio bias at the population and brood level in the greater ani (*Crotophaga major*, hereafter “ani”), a cooperatively breeding Neotropical cuckoo. Anis nest in groups consisting of two to three unrelated pairs, and all individuals in a nesting group provide care to a communal brood laid in a single nest (Riehl 2011). Approximately 20% of groups also contain 1–2 unpaired, non-breeding helpers who contribute to all aspects of parental care, including incubation, nest defense, and provisioning nestlings. Previous studies of this population have found that helpers can be either related to the brood that they help (offspring of the natal group who delay dispersal and assist in raising subsequent broods) or unrelated (immigrants who join the group as unpaired helpers and do not reproduce; Riehl 2021). Related helpers are predominantly male (83%; 24 of 29); little is known about the sex of unrelated helpers, though preliminary data suggest that they are predominantly female (86%; 6 of 7). Unrelated helpers may subsequently reproduce in the groups that they help, but related helpers have never been observed to breed in their natal group. Helpers increase the fitness of breeding adults by defending against nest predators: the presence of each helper reduces the likelihood of nest predation by 11–15% (Riehl and Smart 2022), and nestling growth rates (in terms of mass, tarsus length, and culmen length) are slightly higher at nests with helpers (CR and A.G. Savagian, unpubl. data). Therefore, anis satisfy two key assumptions of the repayment hypothesis: (1) one sex is more likely than the other to delay dispersal and become a non-breeding helper (Gowaty and Lennartz 1985) and (2) helpers enhance the fitness of the breeders that they assist (Griffin et al. 2005). Since helping is male-biased in anis, the repayment hypothesis predicts a male-biased offspring sex ratio, particularly in groups that lack helpers.

Although the repayment hypothesis predicts a bias in sex allocation at the brood level, environmental factors do not

affect each individual in a brood equally (Carranza 2004). In altricial birds, this can occur when incubation begins before the clutch is complete, resulting in asynchronous hatching and an age-based size hierarchy among nestlings (reviewed in Magrath 1990). The size of a nestling is generally predictive of its competitive ability in the nest, so size hierarchies created by asynchronous hatching are typically maintained as late-hatched nestlings grow more slowly, fledge at a lower weight, and starve more frequently (Bortolotti 1986; Slagsvold 1986; Clotfelter et al. 2000; Lago et al. 2000; Maddox and Weatherhead 2008). This dynamic is relevant to the study of sex allocation in species that are sexually size dimorphic since the larger and smaller sexes may be affected differentially by their position in the hatch order. In anis, incubation generally begins after the laying of the penultimate egg; however, incubation can also occur sporadically earlier during the egg-laying stage (Riehl 2020). Because of this, ani broods can hatch over a period of 1–4 days and may contain chicks of several distinct age cohorts (or a cohort of same-aged chicks and a single, late-hatching chick that is smaller than its nestmates) (Riehl 2020). Additionally, adult anis are slightly size dimorphic by sex, with males weighing 6% more than females (Riehl 2020). This dimorphism typically develops by the 6th day of the nestling period (CR and A.G. Savagian, unpubl. data), which suggests that the sexes might impose different immediate energetic costs on parents. This differential cost is especially pertinent to late-hatching nestlings because late-hatched ani nestlings are smaller and more vulnerable to starvation than their larger, early-hatched nestmates (Riehl 2016).

A number of general models have been developed to understand which sex would be optimally placed in a given position in the hatch order (Carranza 2004; Uller 2006), but, unlike the repayment hypothesis, we are unable to validate all the assumptions underlying these models in anis since we lack sufficient data on how the survival of male and female offspring varies with respect to the brood sex ratio and position in hatch order. Nevertheless, because the predictions of these models differ with respect to the sex of late-hatched nestlings, we can determine which (if any) is consistent with our long-term nest monitoring data. The predictions that these models make depend on the nature of interactions between nestlings. Two non-mutually exclusive factors that likely impact the survival of late-hatched nestlings are (1) the direct energetic cost associated with raising male vs. female offspring or (2) the ability of a late-hatched nestling to compete for food. For this reason, adaptive arguments can be made for either a male or female bias in late-hatched nestlings (Hasselquist and Kempenaers 2002), as follows.

Male offspring might be more costly to parents simply because their larger size requires more parental provisioning (Fiala and Congdon 1983), which typically decreases with hatch order (Carranza 2004). Likewise, as observed

in icterids, the larger sex (males) might take longer to reach adult size (Bancroft 1984) and/or fledge (Richter 1983). For this reason, the intra-brood sharing-out hypothesis (Carranza 2004) predicts that parents might best prevent the loss of late-hatched ani nestlings by making them female, the energetically inexpensive sex. However, although the larger sex is potentially more energetically costly to parents, it is also often better able to compete with nestmates for food (Anderson et al. 1993). To maximize the number of offspring that they successfully raise, parents might use sex allocation to alter the competitive environment within their nests (Carranza 2004; Uller 2006). Specifically, parents may manipulate the sex of late-hatched nestlings to either compensate for competitive asynchronies in a brood (e.g., ameliorating the situation of late-hatched nestlings; Uller 2006) or exacerbate competitive asynchronies (e.g., adaptive brood reduction, Lack 1947; facilitating sibling cannibalism, Soler et al. 2022). Thus, the intra-brood competitive equilibrium hypothesis (Uller 2006) predicts a bias for producing males as late-hatching nestlings since their increased size would reduce competitive asymmetries in the brood and their probability of starvation. Since competition for resources between ani nestlings increases with brood size and with the degree of hatching asynchrony (Riehl 2016), we might expect more pronounced sex biases in hatching order in these conditions. However, even pronounced sex biases with respect to hatch order do not necessarily result in a population-level bias (e.g., Bortolotti 1986; Bednarz and Hayden 1991; Legge et al. 2001; Badyaev et al. 2002; Xirouchakis et al. 2022).

In this paper, we leverage a long-term dataset on the breeding biology of anis in central Panama to test the predictions of three hypotheses at the level of the population and the brood. The repayment hypothesis predicts that (1) population-level sex ratios should be biased toward males (the helping sex) and/or (2) brood sex ratios should be biased toward males in groups that lack helpers. By contrast, the intra-brood sharing-out and intra-brood competitive equilibrium hypotheses predict that late-hatched nestlings should be more likely to be female (the energetically inexpensive sex) and male (the more competitive sex), respectively. Likewise, this bias in late-hatched nestlings should increase with brood size and the degree of hatching but not necessarily result in a biased population-level sex ratio. Of course, there are many additional hypotheses for deviations from Fisherian sex ratios that could apply to anis (reviewed in Cockburn et al. 2002). For example, the models developed by Uller (2006) and Carranza (2004) generalize beyond the specific set of circumstances that our data allow us to explore. While we cannot definitively rule out alternative hypotheses, the contrasting predictions of the present framework permit us to determine if our data are consistent with a subset of hypotheses germane to our study system.

Methods

Study population

We monitored a nesting population of anis in the Barro Colorado Nature Monument, central Panama, from 2007–2019; this study contains data from 2007–2009 and 2012–2019. Monitoring efforts in 2010–2011 were insufficient for inclusion in this dataset. The study area included Barro Colorado Island and five nearby mainland peninsulas (9.15°N, 79.85°W). Anis range from Panama to northern Argentina; breeding is restricted to the shores of lakes and rivers, where they nest in emergent vegetation or vegetation overhanging the water. Nests are large open-cup structures made from sticks and are typically located < 4 m above the water's surface (Riehl and Jara 2009). In this population, approximately 80% of nesting groups contain two breeding pairs and 20% contain three breeding pairs. Groups with more than three pairs are extremely rare (~ 1%) and lone pairs have never been observed to attempt breeding. Approximately 20% of breeding groups also contain one (rarely two) unpaired helper, who stay with the breeding group for 1 year (65%), 2 years (31%), or 3 years (4%). Total group size therefore ranges from 4–8 adults, with the modal group size being 4 adults (mean \pm SE = 4.75 \pm 0.05). Breeding females synchronize egg laying in their communal clutches through a highly stereotyped pattern of egg ejection whereby each female ejects the eggs of other females in her nesting group until she starts laying eggs herself. Once a female begins laying, she ceases to eject eggs. As a result, the first egg laid in the communal nest is always ejected, and eggs cannot accumulate in the nest until all females have started laying. Females therefore contribute approximately equal numbers of eggs to the communal clutch. Each female contributes 3–5 eggs to the incubated clutch, so communal clutch size ranges from 6–15 eggs depending on the number of laying females (Vehrencamp 1977; Riehl 2011).

Nest monitoring

We located and monitored ani nests during each breeding season (June–September); most nests were located before egg laying began since ani groups typically remain on the same territory for multiple years (Riehl and Strong 2018). We visited nests every 2–3 days until signs of egg laying were noted (such as gravid females or the addition of green leaves to a nest; Riehl and Jara 2009). We then visited nests daily during egg laying, every 2–3 days during incubation, daily during the first 6 days of the nestling period, and every 2–3 days once nestlings had fledged (which occurs 6–14 days after hatching). We marked nestlings on the day that they hatched with temporary, expandable plastic leg bands (from 2007 to 2009) or non-toxic nail polish (from

2012 to 2019). When nestlings were 2–3 days of age, we collected small (< 100 μ L) blood samples by brachial venipuncture. Blood samples were stored in lysis buffer at room temperature for up to 1 year (White and Densmore 1992). When nestlings were 4–5 days old, we permanently banded them with colored metal leg bands. We did not collect genetic samples from embryos in eggs that did not hatch or from dead nestlings. For this reason, our study reports secondary, not primary, sex ratios (the ratio of male to female offspring that survived to be sampled).

We determined how many adults belonged to each breeding group by recording the number of adults observed at each nest, by marking adults at a subset of nests (with either color bands or temporary, non-toxic paint; Maurer et al. 2008, 2011), and by noting the timing of egg laying, which is highly predictable (Riehl 2010). Adults were assigned as members of breeding pairs or as unpaired adults through behavioral observations (anis are socially monogamous and pair bonds can be detected through behaviors such as allopreening and mate guarding; Riehl and Jara 2009). Non-breeding helpers were identified by their unique color-band combinations and (in some cases of unrelated helpers) by observations of groups with an odd number of individuals.

Molecular sexing and sample sizes

We extracted DNA from blood samples using Qiagen DNEasy Blood and Tissue Isolation Kits (2007–2009) and Omega Bio-tek E.Z.N.A. Tissue DNA kits (2012–2019). We determined the sex of nestlings via PCR-based amplification using the P2 and P8 primer sequences (Griffiths et al. 1998). We were able to determine the sex of 88.2% of nestlings sampled via gel electrophoresis ($N = 553$ of 627). Sex determination of nestlings was blind since information about potential predictors (e.g., position in hatch order and helper presence) was not made available to laboratory technicians during molecular sexing tests. Nestlings whose sex could not be determined (due to poor amplification or ambiguous resolution on the gel) were excluded from statistical analyses. The nestlings whose sex could be determined came from 109 unique broods and 67 nest locations. Since some broods had incomplete information related to the explanatory variables of interest (e.g., hatch order, helper presence, etc., described below), the final sample size used in statistical models included 472 nestlings, 87 broods, and 56 nest locations.

Statistical analyses

To investigate the possibility of a sex ratio bias at the population level, we compared the number of male and female

nestlings observed across all years of the study using a binomial test (Cordero et al. 2000; Woxvold and Magrath 2005; Kingma et al. 2011) as well as a Wilcoxon signed-rank test (Lessells et al. 1996). The former suffers from inflated type I error when individual observations (i.e., the sex of nestlings) are not statistically independent, while the latter protects against type I error inflation (Neuhäuser 2004). To control for the effects of brood and year, we also examined the population-level sex ratio by constructing a generalized linear mixed-effects model with a logit link using the *glmer* function in the *lme4* package (Bates et al. 2015) in R version 4.2.2 (R Core Team 2022). The model included nestling sex (coded as “0” for females and “1” for males) as the response variable as well as nest location and year (nested within nest location) as random effects. We included no fixed effects in this model and calculated the odds ratio of the intercept, which may deviate from 1 (a 1:1 ratio of male and female offspring) if a population-level sex bias is present.

To investigate the possibility of facultative sex ratio biases at the brood level, we constructed models predicting the probability that a nestling is a male. Our goal was to determine which characteristics of a nesting attempt (if any) influenced the sex of individual nestlings. We created additional generalized linear mixed-effects models with a logit link with nestling sex as the response variable as well as nest location and year as random effects to control for repeated measures from the same nesting group across years. Fixed effects included hatch order, hatching synchrony, brood size, clutch size, the presence of helpers, the number of breeding pairs, and the interaction between synchrony and hatch order. Because multiple nestlings often hatch on the same day and broods varied in size, we categorized hatch order as “first,” “middle,” and “last,” with “first” and “last” describing the absolute earliest and latest positions in the hatch order respectively and “middle” describing all intermediate positions (Riehl 2016). Hatch order within each brood was typically determined through daily nest checks or by the relative size of nestlings within the brood for nests that were not checked daily during the hatching period. We define hatching asynchrony as the range of calendar days over which hatching occurred in a nest. Brood size refers to the number of nestlings that hatched in a nest. Clutch size refers to the number of eggs incubated in a focal nest and does not include eggs that were ejected from the nest. Helper presence is a binary variable (“0” or “1”) that indicates whether or not a nesting group had at least one non-breeding helper. Finally, the number of breeding pairs refers to the number of monogamous pairs of breeding anis that were observed at a nest while it was active and contributed to the communal clutch of eggs (either two or three pairs). This distinction was unambiguous in all nesting groups except one (group A6 in 2017). This group consisted of three behaviorally monogamous pairs and one unpaired helper, but one of the pairs did

not contribute eggs to the communal clutch despite attending the nest. We speculate that this non-breeding pair was in the process of joining the breeding group and consider “A6” a three-pair group in our analyses.

Model selection was conducted using a “best subsets” method. Candidate models were compared to every possible model including a subset of the terms. Including a null model with no fixed effects and a global model containing all possible fixed effects, we considered 80 candidate models. We did not consider candidate models that included the synchrony by hatch order interaction term unless they also contained synchrony and hatch order separately as fixed effects (Nelder 1977). Candidate models were evaluated based on Akaike’s information criterion adjusted for finite sample sizes (AICc) (Burnham and Anderson 2002). Models that differed from the top model by less than 2 AICc units were considered to potentially have explanatory value unless they differed from the top model by the addition of a single parameter (Arnold 2010). We verified that multicollinearity was not a concern by calculating variable inflation factors (VIFs) for our global model (all VIFs < 4 as per Garson (2012); Table S1). Likewise, we evaluated the fit of our models by using the “DHARMA” package to visualize model residuals (Fig. S1; Hartig 2022). We used the “SIMR” package (Green and Macleod 2016) to calculate the power for our models using effect sizes from previous studies of the repayment hypothesis summarized by Khwaja et al. (2017; Table S2). Our sample size was sufficient to detect a small effect size (0.2) with a power of 0.96. We did not pursue brood-level models of sex allocation (e.g., a combined response variable consisting of the number of males and females in a brood; Bartlow et al. 2021) since it was rarely possible to sample all the ani nestlings in a brood. Due to the large size of many broods, hatching asynchrony, high nestling mortality rates, and the small window of time in which nestlings can be safely sampled, we were able to collect samples from every nestling in only 37.6% of broods (41 of 109).

The repayment hypothesis predicts a male-biased sex ratio at the population level and/or a male bias in groups lacking helpers. If this hypothesis were supported, we expected that helper presence should emerge as a significant predictor of nestling sex in our model selection framework. By contrast, the intra-brood sharing-out and intra-brood competitive equilibrium hypotheses both predict a bias in last-hatched nestlings (female and male, respectively) but not necessarily at the population level. The sex bias of late-hatched nestling would be most pronounced in situations with high competition among nestlings. If one of these hypotheses were supported, we expected that clutch size, brood size, hatch order, and/or hatching synchrony should emerge as significant predictors of nestling sex.

Results

Population-level sex ratio

We found no evidence that the sex ratio of nestlings in the population (266 of 553 nestlings, 48.10%, were male) deviated from the expected Fisherian ratio of 1:1 (binomial test: $p=0.40$; Wilcoxon’s signed-rank test: $V=1882$, $p=0.32$). Similarly, a generalized linear mixed model of nestling sex with no fixed effects confirmed an equal male–female ratio (OR of intercept = 1.03, 95% CI = 0.81–1.31). The population-level nestling sex ratio did vary by year, with significant female biases in 6 of 11 years (2007, 2009, 2013–2015, 2019); male biases were not observed in any of the 10 years (Fig. 1). However, the 6 years with female-biased sex ratios were also typically the years with the lowest sample sizes (mean sample size in female-biased

and unbiased years is 28 and 77 nestlings, respectively), which precluded further quantitative analysis.

Facultative sex ratio adjustment

Our model selection procedures found no evidence of facultative sex ratio adjustment compatible with our hypotheses. Contrary to predictions, neither helper presence nor hatch order improved the fit of the model predicting nestling sex, and no combination of fixed effects significantly outperformed the null model (Table 1; Table S3). Data visualization further confirms these trends: nests without helpers were not more likely to produce males (contrary to the prediction of the repayment hypothesis; Fig. 2a) nor did hatch order affect sex allocation (contrary to the predictions of

Fig. 1 Sex ratio of nestlings during each year of our study. Error bars show 95% confidence intervals. The dotted line indicates a 50:50 sex ratio, and the number of nestlings sexed in each year is shown above the error bars for each year

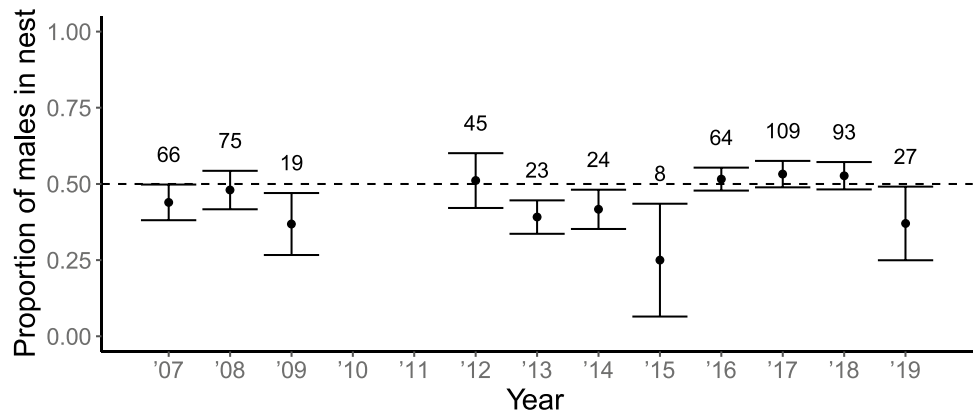


Table 1 Best subset models predicting the sex of individual nestlings

Fixed effects	$\Delta AICc$	AICc	χ^2	P	w	Pseudo R^2
Hatch order + clutch size	0.000	656.314	7.027	0.071	0.058	0.157
Clutch size	0.133	656.447	2.799	0.094	0.054	0.152
Hatch order	0.703	657.017	4.272	0.118	0.041	0.154
Hatch order + breeding pairs	0.952	657.266	6.075	0.108	0.036	0.156
Breeding pairs	1.062	657.376	1.870	0.172	0.034	0.150
Hatch order + brood size	1.266	657.58	5.761	0.124	0.031	0.156
Brood size	1.425	657.739	1.507	0.220	0.028	0.150
Clutch size + helper	1.470	657.784	3.505	0.173	0.028	0.153
Clutch size + synchrony	1.652	657.966	3.323	0.190	0.025	0.152
Hatch order + helper	1.967	658.281	5.060	0.167	0.022	0.155
Global	9.242	665.556	10.284	0.328	0.001	0.161
Null	113.993	770.307	-	-	0.000	0.000

All models are generalized linear mixed effect models with nest location and year included as a random intercept. Each model is compared to a null model run on the same dataset including only random effects using a likelihood ratio test. Models with $\Delta AICc < 2$ are shown as well as global and null models. All continuous variables (i.e., clutch size, brood size, synchrony) were scaled and centered to reduce multicollinearity

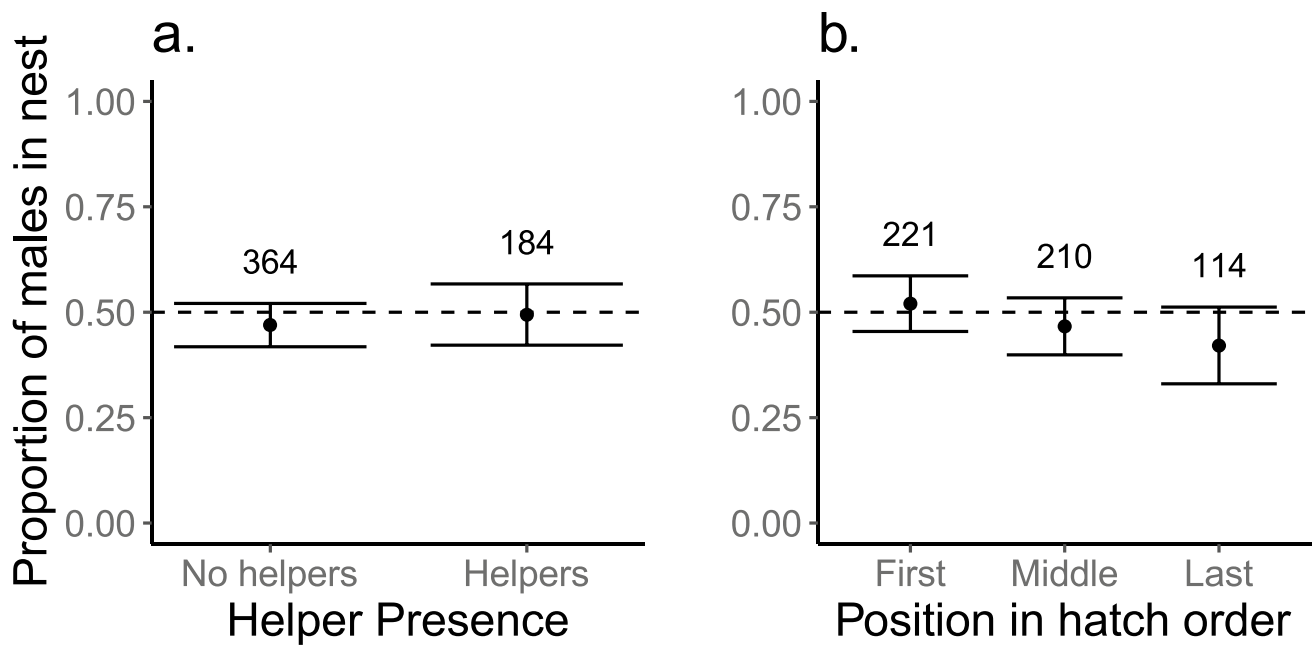


Fig. 2 Sex ratio of nestlings with respect to **a** whether or not a helper was observed at their nest and **b** position in hatch order. In both, error bars show 95% confidence intervals, the dotted line indicates a

50:50 sex ratio, and the number of nestlings sexed in each category is shown above each error bar

either the intra-brood sharing-out or intra-brood competitive equilibrium hypotheses; Fig. 2b).

Discussion

The results of this study reveal little evidence consistent with adaptive sex allocation in cooperatively breeding anis. The population-level sex ratio was unbiased, and we failed to detect an effect of hatch order or the presence of helpers. The lack of a pronounced population-level sex ratio bias in our study is perhaps unsurprising, given the frequency-dependent selection on sex ratios described by the Düsing-Fisher model (Düsing 1883, 1884; Fisher 1930). Variations in selective pressures acting on the sex allocation of individual females make sex ratios at the population level inherently difficult to predict (Frank 1990; West and Sheldon 2002). Deviations from parity in nestling sex ratios are fairly rare at the population level in birds (but see Bednarz and Hayden 1991; Clarke et al. 2002; Tryjanowski et al. 2011) and, in some cases, attributable to selective reporting (Palmer 2000).

A key insight that has emerged from the literature on adaptive sex allocation is that parents must be able to accurately predict the conditions that their nestlings will encounter during development (West and Sheldon 2002; West et al. 2002). The hypotheses investigated in this study assume that anis can predict (1) the presence of helpers at their nest during a breeding season, (2) the order in which their eggs

will hatch, and (3) the competitive environment within their nests. We now discuss whether these assumptions are met in our study system.

With regards to the first assumption, helpers at ani nests may be either non-dispersed 1-year-olds from a previous brood (which are typically male) or unrelated immigrants (which are typically female). However, both related and unrelated helpers are usually present in the breeding group for weeks or months before the onset of breeding. Related helpers stay with their natal group for the entire year, and unrelated helpers usually join the breeding group during the non-breeding season. Members of breeding groups, including helpers, typically roost and forage together and remain in close contact year round. Therefore, it seems reasonable to assume that adult females should be able to predict whether they will be assisted by a helper at the time that sex allocation occurs. Similarly, although the degree of hatching asynchrony in a nest is not entirely predictable at the time of sex allocation (since this depends on when incubation begins), the position of an egg in the laying order of the communal clutch is closely correlated with its position in the hatch order. An exception to this pattern is early-laid eggs. Since anis use egg ejection to synchronize egg laying and eggs are ejected until all females have begun laying, there is a degree of uncertainty regarding which egg will be the first to remain in the nest (Riehl 2010). Although egg ejection might complicate fine-scale sex allocation strategies in early-laid eggs (e.g., first- vs. second-hatched young), the second assumption also appears to be reasonably well supported in anis.

The third assumption, that adults can predict the environmental conditions that their offspring will experience, is more complex. The degree of competition among nestlings in a brood is likely determined by several factors, including hatch order, synchrony, brood size, and food availability, all of which could considerably alter the fitness payoffs of producing male vs. female offspring. Although we lack the data necessary to examine some of these factors (particularly resource availability), previous work on this population suggests that nestling competition is most severe in large clutches and for late-hatching nestlings (Riehl 2016). Brood size may be more predictable than hatching synchrony and is correlated with the number of breeding adults in anis, so it is possible that adult females may be able to estimate the size of the brood at the time of sex allocation. Nevertheless, it is important to note that, although an ani might be able to control the sex of her offspring, the sex of the offspring of her co-breeders is likely outside of her control. This distinction between the clutch of an individual female and the communal clutch is important because the fitness of a sex allocation strategy may depend on the sex ratio of the communal clutch (e.g., producing more male offspring may only increase fledging success if co-breeders do not also produce more male offspring). This additional uncertainty likely reduces the potential value of facultative sex ratio adjustment in this species.

Finally, there are several reasons why sex allocation might be adaptive in theory but difficult to detect in practice, due to methodological or biological constraints. In our study, we report secondary, not primary, sex ratios since we were unable to determine the sex of unincubated eggs and blood sampling of all nestlings in a brood was not always possible. We avoided collecting blood samples from nestlings that appeared very weak and near death, which reduced our sample size of late-hatched individuals key to two of the adaptive hypotheses tested. Likewise, since ani nestlings develop at a remarkably fast rate and fledge very early for altricial birds of their size, our understanding of how male and female growth patterns differ is limited to a window of 6 days. For this reason, the growth curves of ani nestlings do not reach an asymptote (e.g., Richter 1983; Bancroft 1984), which leaves open the possibility of more complex growth dynamics outside of the nest that could impact competition between male and female fledglings.

Biologically, it is unlikely that the selection on sex ratios responds to a single, static factor (Cockburn et al. 2002). For this reason, the testing of quantitative predictions and further study of physiology and genetics within individual study species could greatly clarify the question of adaptive sex allocation in vertebrates (Godfray and Werren 1996). Despite decades of research, the mechanism by which vertebrates facultatively adjust primary sex ratios remains unknown and, therefore, is often neglected in models (Pen and Weissing 2002) even though a mechanism with a relatively small cost could overcome the benefits of adjusting the sex of offspring (Pen et al. 1999).

Additionally, since the three hypotheses that we test are non-mutually exclusive, it is possible that they interact in more complex ways. For example, Moreno-Rueda et al. (2017) find support for both the intra-brood sharing-out and intra-brood competitive equilibrium hypotheses within the same population (the former being observed in smaller clutches and the latter in larger). However, studies testing a larger number of adaptive hypotheses note that the absence of adaptive manipulation of sex ratios is more probable than the simultaneous action and concealment of several selective pressures (Kingma et al. 2011).

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Author contribution CR conceived the study, collected field data, conducted genetic sexing, and managed the study system. TCH organized the dataset, conducted statistical analyses, and created figures. Both authors wrote the paper and contributed to the interpretation and presentation of data.

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Data availability The dataset analyzed during the current study is available in the figshare repository, 10.6084/m9.figshare.22816907.

Code availability The R code used in this study is available in the figshare repository, 10.6084/m9.figshare.21761462.

Declarations

Ethics approval The research in this study was approved by the Institutional Animal Care and Use Committee of the Smithsonian Tropical Research Institute. Genetic samples were collected and exported with approval from the Ministerio de Ambiente de Panamá and imported to the USA with approval from the US Department of Agriculture. All applicable international, national, and/or institutional guidelines for the use of animals were followed.

Competing interests The authors declare no competing interests.

References

- Anderson DJ, Budde C, Apanius V, Martinez-Gomez JE, Bird DM, Weathers WW (1993) Prey size influences female competitive dominance in nestling American kestrels (*Falco sparverius*). *Ecology* 74:367–376. <https://doi.org/10.2307/1939299>
- Arnold TW (2010) Uninformative parameters and model selection using Akaike's information criterion. *J Wildlife Manage* 74:1175–1178. <https://doi.org/10.2193/2009-367>
- Badyaev AV, Hill GE, Beck ML, Dervan AA, Duckworth RA, McGraw KJ, Nolan PM, Whittingham LA (2002) Sex-biased hatching order and adaptive population divergence in a passerine bird. *Science* 295:316–318. <https://doi.org/10.1126/science.1066651>
- Bancroft GT (1984) Growth and sexual dimorphism of the boat-tailed grackle. *Condor* 86:423–432. <https://doi.org/10.2307/1366822>
- Bartlow AW, Jankowski MD, Hathcock CD, Ryti RT, Reneau SL, Fair JM (2021) Sex ratio of western bluebirds (*Sialia mexicana*) is mediated by phenology and clutch size. *Ibis* 163:977–989. <https://doi.org/10.1111/ibi.12935>
- Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bednarz JC, Hayden TJ (1991) Skewed brood sex ratio and sex-biased hatching sequence in Harris's hawks. *Am Nat* 137:116–132. <https://doi.org/10.1086/285149>
- Berg EC (2004) A test of sex-ratio biasing in the white-throated magpie-jay, a cooperative breeder with female helpers. *Condor* 106:299–308. <https://doi.org/10.1650/7404>
- Bortolotti GR (1986) Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *Am Nat* 127:495–507. <https://doi.org/10.1086/284498>
- Burnham K, Anderson D (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Carranza J (2004) Sex allocation within broods: the intrabrood sharing-out hypothesis. *Behav Ecol* 15:223–232. <https://doi.org/10.1093/beheco/ahr004>
- Charnov EL (1982) The theory of sex allocation. *Monogr Popul Biol* 18:1–355. <https://doi.org/10.2307/j.ctvx8b6km>
- Clarke MF, Jones DA, Ewen JG, Robertson RJ, Griffiths R, Painter J, Boag PT, Crozier R (2002) Male-biased sex ratios in broods of the cooperatively breeding bell miner *Manorina melanophrys*. *J Avian Biol* 33:71–76. <https://doi.org/10.1034/j.1600-048X.2002.330111.x>
- Clofelter ED, Whittingham LA, Dunn PO (2000) Laying order, hatching asynchrony and nestling body mass in tree swallows *Tachycineta bicolor*. *J Avian Biol* 31:329–334. <https://doi.org/10.1034/j.1600-048X.2000.310308.x>
- Cockburn A, Double MC (2008) Cooperatively breeding superb fairy-wrens show no facultative manipulation of offspring sex ratio despite plausible benefits. *Behav Ecol Sociobiol* 62:681–688. <https://doi.org/10.1007/s00265-007-0492-1>
- Cockburn A, Legge S, Double MC (2002) Sex ratios in birds and mammals: can the hypotheses be disentangled? In: Hardy ICW (ed) Sex ratios: concepts and research methods. Cambridge University Press, Cambridge, pp 266–286
- Cordero PJ, Griffith SC, Aparicio JM, Parkin DT (2000) Sexual dimorphism in house sparrow eggs. *Behav Ecol Sociobiol* 48:353–357. <https://doi.org/10.1007/s002650000252>
- Darwin CR (1871) The descent of man, and selection in relation to sex. John Murray, London
- Düsing C (1883) Die Faktoren, welche die Sexualität entscheiden. *Jena Z Naturwiss* 16:428–464
- Düsing C (1884) Die Regulierung des Geschlechtsverhältnisses bei der Vermehrung der Menschen, Tiere und Pflanzen. Fischer, Jena, Germany
- Emlen ST, Emlen JM, Levin SA (1986) Sex-ratio selection in species with helpers-at-the-nest. *Am Nat* 127:1–8. <https://doi.org/10.1086/284463>
- Fiala KL, Congdon JD (1983) Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. *Ecology* 64:642–647. <https://doi.org/10.2307/1937183>
- Fisher RA (1930) The genetical theory of natural selection, 2nd edn. Clarendon, Oxford
- Frank SA (1990) Sex allocation theory for birds and mammals. *Annu Rev Ecol Syst* 21:13–55. <https://doi.org/10.1146/annurev.es.21.110190.000305>
- Garson GD (2012) Testing statistical assumptions. Statistical Associates Publishing, Asheboro, NC
- Godfray HCJ, Werren JH (1996) Recent developments in sex ratio studies. *Trends Ecol Evol* 11:59–63. [https://doi.org/10.1016/0169-5347\(96\)81043-3](https://doi.org/10.1016/0169-5347(96)81043-3)
- Gowaty PA, Lennartz MR (1985) Sex ratios of nestling and fledgling red-cockaded woodpeckers (*Picoides borealis*) favor males. *Am Nat* 126:347–353. <https://doi.org/10.1086/284421>
- Green P, Macleod CJ (2016) SIMR: an R package for power analysis of generalized linear mixed models by simulation. *Methods Ecol Evol* 7:493–498. <https://doi.org/10.1111/2041-210X.12504>
- Griffin AS, Sheldon BC, West SA (2005) Cooperative breeders adjust offspring sex ratios to produce helpful helpers. *Am Nat* 166:628–632. <https://doi.org/10.1086/491662>
- Griffiths R, Double MC, Orr K, Dawson RJG (1998) A DNA test to sex most birds. *Mol Ecol* 7:1071–1075. <https://doi.org/10.1046/j.1365-294x.1998.00389.x>
- Hartig F (2022) DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.6, <https://CRAN.R-project.org/package=DHARMA>
- Hasselquist D, Kempenaers B (2002) Parental care and adaptive brood sex ratio manipulation in birds. *Phil Trans R Soc B* 357:363–372. <https://doi.org/10.1098/rstb.2001.0924>
- Herre EA (1987) Optimality, plasticity and selective regime in fig wasp sex ratios. *Nature* 329:627–629. <https://doi.org/10.1038/329627a0>
- Khwaja N, Hatchwell BJ, Freckleton RP, Green JP (2017) Sex allocation patterns across cooperatively breeding birds do not support predictions of the repayment hypothesis. *Am Nat* 190:547–556. <https://doi.org/10.1086/693532>
- Kingma SA, Hall ML, Peters A (2011) No evidence for offspring sex-ratio adjustment to social or environmental conditions in cooperatively breeding purple-crowned fairy-wrens. *Behav Ecol Sociobiol* 65:1203–1213. <https://doi.org/10.1007/s00265-010-1133-7>
- Komdeur J (2004) Sex-ratio manipulation. In: Koenig WD, Dickinson JL (eds) Ecology and behaviour of cooperative breeding in birds. Cambridge University Press, Cambridge, pp 102–116
- Komdeur J, Daan S, Tinbergen J, Mateman C (1997) Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. *Nature* 385:522–525. <https://doi.org/10.1038/385522a0>
- Lack D (1947) The significance of clutch-size. *Ibis* 89:302–352. <https://doi.org/10.1111/j.1474-919X.1947.tb04155.x>
- Lago K, Johnson LS, Albrecht DJ (2000) Growth of late-hatched, competitively disadvantaged nestling house wrens relative to their older, larger nestmates. *J Field Ornithol* 71:676–685. <https://doi.org/10.1648/0273-8570-71.4.676>
- Legge S, Heinsohn R, Double MC, Griffiths R, Cockburn A (2001) Complex sex allocation in the laughing kookaburra. *Behav Ecol* 12:524–533. <https://doi.org/10.1093/beheco/12.5.524>
- Leimar O (1996) Life-history analysis of the Trivers and Willard sex-ratio problem. *Behav Ecol* 7:316–325. <https://doi.org/10.1093/beheco/7.3.316>
- Lessells CM, Mateman AC, Visser J (1996) Great tit hatchling sex ratios. *J Avian Biol* 27:135–142. <https://doi.org/10.2307/3677142>
- Ligon JD, Ligon SH (1990) Female-biased sex ratio at hatching in the green woodhoopoe. *Auk* 107:765–771. <https://doi.org/10.2307/4088009>

- Maddox JD, Weatherhead PJ (2008) Egg size variation in birds with asynchronous hatching: is bigger really better? *Am Nat* 171:358–365. <https://doi.org/10.1086/527500>
- Magrath RD (1990) Hatching asynchrony in altricial birds. *Biol Rev* 65:587–622. <https://doi.org/10.1111/j.1469-185X.1990.tb01239.x>
- Maurer G, Smith C, Süsser M, Magrath RD (2008) Solo and duet calling in the pheasant coucal: sex and individual call differences in a nesting cuckoo with reversed size dimorphism. *Aust J Zool* 56:143–149. <https://doi.org/10.1071/ZO08049>
- Maurer G, Double MC, Milenkaya O, Süsser M, Magrath RD (2011) Breaking the rules: sex roles and genetic mating system of the pheasant coucal. *Oecologia* 167:413–425. <https://doi.org/10.1007/s00442-011-2002-4>
- Moreno-Rueda G, Campos F, Gutiérrez-Corchero F, Hernández MÁ (2017) Hatching order and sex ratio in southern grey shrike *Lanius meridionalis* in relation to clutch size. *Ibis* 159:230–234. <https://doi.org/10.1111/ibi.12427>
- Nam KB, Meade J, Hatchwell BJ (2011) Brood sex ratio variation in a cooperatively breeding bird. *J Evol Biol* 24:904–913. <https://doi.org/10.1111/j.1420-9101.2011.02228.x>
- Nelder JA (1977) A reformulation of linear models. *J R Stat Soc A* 140:48–77. <https://doi.org/10.2307/2344517>
- Neuhäuser M (2004) Tests for a biased sex ratio when the data are clustered. *Environ Ecol Stat* 11:295–304. <https://doi.org/10.1023/B:EEST.0000038017.58293.c0>
- Palmer AR (2000) Quasi-replication and the contract of error: lessons from sex ratios, heritabilities and fluctuating asymmetry. *Annu Rev Ecol Syst* 31:441–480. <https://doi.org/10.1146/annurev.ecolsys.31.1.441>
- Patterson CB, Erckmann WJ, Orians GH (1980) An experimental study of parental investment and polygyny in male blackbirds. *Am Nat* 116:757–769. <https://doi.org/10.1086/283668>
- Pen I, Weissing FJ (2000) Sex-ratio optimization with helpers at the nest. *Proc R Soc Lond B* 267:539–543. <https://doi.org/10.1098/rspb.2000.1034>
- Pen I, Weissing FJ (2002) Optimal sex allocation: steps towards a mechanistic theory. In: Hardy I (ed) *Sex ratios: concepts and research methods*. Cambridge University Press, Cambridge, pp 26–46
- Pen I, Weissing FJ, Daan S (1999) Seasonal sex ratio trend in the European kestrel: an evolutionarily stable strategy analysis. *Am Nat* 153:384–397. <https://doi.org/10.1086/303183>
- Queller DC (2006) Sex ratios and social evolution. *Curr Biol* 16:R664–R668. <https://doi.org/10.1080/10926771.2013.789095>
- R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Richter W (1983) Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics (yellow-headed blackbird *Xanthocephalus xanthocephalus*). *Am Nat* 121:158–171. <https://doi.org/10.1086/284048>
- Riehl C (2010) Egg ejection risk and hatching asynchrony predict egg mass in a communally breeding cuckoo, the greater ani (*Crotophaga major*). *Behav Ecol* 21:676–683. <https://doi.org/10.1093/beheco/arq038>
- Riehl C (2011) Living with strangers: direct benefits favour non-kin cooperation in a communally nesting bird. *Proc R Soc Lond B* 278:1728–1735. <https://doi.org/10.1098/rspb.2010.1752>
- Riehl C (2016) Infanticide and within-clutch competition select for reproductive synchrony in a cooperative bird. *Evolution* 70:1760–1769. <https://doi.org/10.1111/evo.12993>
- Riehl C (2021) Evolutionary origins of cooperative and communal breeding: lessons from the crotophagine cuckoos. *Ethology* 127:827–836. <https://doi.org/10.1111/eth.13149>
- Riehl C, Jara L (2009) Natural history and reproductive biology of the communally breeding greater ani (*Crotophaga major*) at Gatún Lake, Panama. *Wilson J Ornithol* 121:679–687. <https://doi.org/10.1676/09-017.1>
- Riehl C, Smart ZF (2022) Climate fluctuations influence variation in group size in a cooperative bird. *Curr Biol* 32:4264–4269.e3. <https://doi.org/10.1016/j.cub.2022.07.057>
- Riehl C, Strong MJ (2018) Stable social relationships between unrelated females increase individual fitness in a cooperative bird. *Proc R Soc B* 285:20180130. <https://doi.org/10.1098/rspb.2018.0130>
- Riehl C (2020) Greater ani (*Crotophaga major*), version 1.0. In: Schulenberg TS (ed) *Birds of the world*. Cornell Lab of Ornithology, Ithaca, NY. <https://doi.org/10.2173/bow.greani.01>
- Slagsvold T (1986) Asynchronous versus synchronous hatching in birds: experiments with the pied flycatcher. *J Anim Ecol* 55:1115–1134. <https://doi.org/10.2307/4437>
- Soler JJ, Martin-Vivaldi M, Nuhlickova S, Ruiz-Castellano C, Mazonra-Alonso M, Martinez-Renau E, Eckenfellner M, Svetlik J, Hoi H (2022) Avian sibling cannibalism: hoopoe mothers regularly use their last hatched nestlings to feed older siblings. *Zool Res* 43:265–274. <https://doi.org/10.24272/j.issn.2095-8137.2021.434>
- Trivers RL, Hare H (1976) Haplodiploidy and the evolution of the social insect. *Science* 191:249–263. <https://doi.org/10.1126/science.1108197>
- Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90–92. <https://doi.org/10.1126/science.179.4068.90>
- Tryjanowski P, Sparks TH, Bochenski M, Dabert M, Kasprzak M, Kaminski P, Mroczkowski S, Wisniewska E, Jerzak L (2011) Do males hatch first and dominate sex ratios in white stork *Ciconia ciconia* chicks? *J Ornithol* 152:213–218. <https://doi.org/10.1007/s10336-010-0571-3>
- Uller T (2006) Sex-specific sibling interactions and offspring fitness in vertebrates: patterns and implications for maternal sex ratios. *Biol Rev* 81:207–217. <https://doi.org/10.1017/S1464793105006962>
- Vehrencamp SL (1977) Relative fecundity and parental effort in communally nesting anis, *Crotophaga sulcirostris*. *Science* 197:403–405. <https://doi.org/10.1126/science.197.4301.403>
- West SA (2009) *Sex allocation*. Princeton University Press, Princeton, NJ
- West SA, Sheldon BC (2002) Constraints in the evolution of sex ratio adjustment. *Science* 295:1685–1688. <https://doi.org/10.1126/science.1069043>
- West SA, Reece SE, Sheldon BC (2002) Sex ratios. *Heredity* 88:117–124. <https://doi.org/10.1038/sj.hdy.6800018>
- White PS, Densmore LD (1992) Mitochondrial DNA isolation. In: Hoezel AR (ed) *Molecular genetic analysis of populations: a practical approach*. Oxford University Press, New York, pp 29–58
- Woxvold IA, Magrath MJL (2005) Helping enhances multiple components of reproductive success in the cooperatively breeding apostlebird. *J Anim Ecol* 74:1039–1050. <https://doi.org/10.1111/j.1365-2656.2005.01001.x>
- Xirouchakis SM, Botsidou P, Baxevasi K, Andreou G, Tsaparis D (2022) Brood sex ratio variation in a colonial raptor, the Eleonora's falcon, *Falco eleonora*. *Anim Behav* 195:93–106. <https://doi.org/10.1016/j.anbehav.2022.11.001>

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