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Unexpected sex ratio adjustment in a colonial cooperative bird: pairs with helpers produce more of the helping sex whereas pairs without helpers do not

Abstract For cooperatively breeding species, the most popular and intensely debated explanation for sex ratio variation is the helper repayment hypothesis. It predicts overall sex ratio bias towards the helping sex, and/or facultative adjustment towards the helping sex in absence of helpers. We tested these predictions in a colonial cooperative bird, the sociable weaver *Philetairus socius*. We quantified variation in overall sex ratio, and tested the effects of helping and local breeding conditions on individual sex ratio. To better understand the factors affecting sex ratio variation, we investigated sex-related differences in helping, dispersal behavior, and nestling morphology. Our results did not support the predictions of the helper repayment hypothesis. Indeed, although we found that males are the philopatric helping sex: (1) we did not detect a consistent bias in overall sex ratio; and (2), more importantly, it was pairs with helpers that produced additional males, not pairs without helpers. We propose and discuss different factors that could explain these results.

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Introduction

Several recent studies have provided empirical evidence that animals with chromosomal sex determination can adjust the sex ratio of their offspring in an adaptive way (e.g., Komdeur and Pen 2002). However, and in spite of a recent explosion of sex ratio studies in vertebrates, the results remain conflicting and a general explanation is lacking (see review in Cockburn et al. 2002), suggesting that more studies are needed to understand sex ratio variation. Briefly, the adaptive hypotheses that have been put forward to explain sex ratio variation in birds and mammals fall into one of the following broad categories (reviewed in Cockburn et al 2002; Komdeur and Pen 2002; West and Sheldon 2002). Sex allocation may result from: (1) the frequency-dependent advantage enjoyed by the rarer sex (Fisher 1930); (2) the difference in resource requirements between male and female offspring (Fisher 1930); and (3) the advantage of producing the sex that will benefit the most from the social, heritable or state-dependent status of its parent. For example, females will produce more sons when they are in good conditions if sons benefit more of the higher social status of their mother (Trivers and Willard 1973), or females will produce more sons when they paired with a male advertising high level of heritable quality (e.g. Burley 1981; Sheldon et al. 1999). Sex ratio variation can also be due to the advantage of producing the sex that will increase more the current or future reproductive success of the parents or that will increase their prospects of surviving to reproduce again. When the parents face limited resources, this occurs if there are sex-related differences in cost of production, sibling competition, dispersal, or helping behavior (e.g., Clark 1978; Hamilton 1967; Julliard 2000). Predictions of the hypotheses explaining evolution of sex ratio can often be formulated

at the population level (overall sex ratio) or at the individual level (facultative sex ratio adjustment).

In cooperative breeders, non-breeding adults, often offspring, help the breeding pairs in raising their young. In those cooperative breeders where one offspring sex is both philopatric and helps at the nest, an overproduction of the helping sex is expected when the presence of these helping offspring improves the breeder's life time reproductive success. This hypothesis has been named the helper repayment hypothesis (see Emlen et al. 1986; Lessells and Avery 1987; Koenig and Walters 1999; Pen and Weissing 2000, for different versions of this hypothesis). In its original formulation, this hypothesis explained variation in sex ratio at the population level (i.e., overall sex ratio). However, all sorts of contradictory results have been found by empirical studies investigating sex ratio variation at population level (sex bias towards the helping sex: Malcolm and Marten 1982; Ligon and Ligon 1990; Allainé et al. 2000; Clarke et al. 2002; no bias: Koenig and Dickinson 1986; Walter 1990; Arnold et al. 2001; Koenig et al. 2001; sex bias towards the non helping sex: Komdeur et al. 1997; Ewen et al. 2001). Due to these conflicting results and the technical difficulties of disentangling the large number of opposing selective pressures that act at the population level (Koenig and Walters 1999), an increasing number of studies are now investigating sex ratio variation at the individual level. At the individual level, the helper repayment hypothesis predicts that pairs without helpers will produce more of the helping sex in order to generate helpers.

Such a prediction got supports in at least four bird species (the Seychelles warbler *Acrocephalus seychellensis*: Komdeur et al. 1997; the laughing kookaburra *Dacelo novaeguineae*: Legge et al. 2001; the green woodhoopoe *Phoeniculus purpureus* Ligon and Ligon 1990, and the bell miner *Manorina melanophrys* Ewen et al. 2003). However another study did not find any significant facultative adjustment to presence of helpers in the acorn woodpecker *Melanerpes formicivorus* (Koenig et al. 2001).

In this study we tested the helper repayment hypothesis on a colonial cooperative bird, the sociable weaver *Philetairus socius*. To this end: (1) we investigated whether there were any sex-related differences in (a) helping behavior (helper sex and feeding rate), (b) morphology of nestlings (body mass and tarsus length) and (c) dispersal behavior; (2) we determined whether sex ratio variation occurs at either or both the individual and population levels; and (3) we investigated which factors can lead to sex ratio bias at the individual level. We tested the effect of the presence / absence of helpers and two factors known to influence the sociable weaver's reproductive success: colony size and rainfall.

If the helper repayment hypothesis explains sex allocation in sociable weavers, we should find: (1) a sex difference in helping and dispersal behaviour; (2) an overall sex ratio bias towards the helping sex; and (3) an overproduction of the helping sex by pairs without helpers.

Methods

The study species and population area

The sociable weaver is a colonial cooperative passerine endemic to southern Africa (Mendelsohn and Anderson 1997). At 30 g, it is a relatively long lived bird (up to at least 10 years, 66% annual survival in our population: Covas et al., unpublished data.) that rarely breeds before 3 years of age (Covas 2002; Covas et al., unpublished data). Sociable weavers build a large communal nest with multiple separate chambers that are occupied all year round by pairs, or pairs accompanied by their helpers. Each nest has its own entrance. Sociable weavers are predominantly insectivorous, but also feed on grass seeds (Maclean 1973a).

The study was conducted on Benfontein farm near Kimberley, South Africa (approx. 28°53′S, 24°49′E). The area is semi-arid, experiencing low and unpredictable rainfall (mean±SD: 431± 127 mm per year; $n=96$ years; Weather Bureau, Pretoria). Rainfall seems to be the main determinant of the duration of the breeding season (leading to nine continuous months of reproduction, or no reproduction in a given year), variation in clutch size and fledging success (Covas 2002). Nest predation is the main cause of reproductive failure, with more than 70% of the clutches falling prey to snakes (Covas 2002; Covas et al., unpublished data).

The proportion of nests with helpers varied greatly between years in our study population. In the first season, about 30% of nests had one to two helpers, while in the second season 82% of the nests had one to three (exceptionally four or five) helpers (Covas 2002; Covas and Doutrelant, unpublished data.). In another study in central Namibia, about 50% of the nests had one male helper while the rest had none (Marsden 1999). Microsatellite analyses of paternity suggest that helpers have no access to paternity (Doutrelant et al. unpublished data).

Field methods

Sex ratio data were collected during two consecutive reproductive seasons spanning 1999 to 2001. All nest chambers were inspected every 4–7 days to detect initiation of new clutches. Nests were visited daily near the hatching date until all eggs had hatched. Nine days after hatching (day 9), we took blood samples from the brachial vein of each nestling using a sterile needle and a heparinized capillary tube. We collected blood from 185 nestlings of 63 broods from 14 colonies. These colonies each comprised between 15 and 70 birds and at least 5–15 families.

To investigate for potential sex-related differences in the costs of rearing, we recorded the number of fledglings alive at day 17, and measured their tarsus and body mass. The nests were last visited 17 days after hatching because sociable weaver nestlings may fledge prematurely if disturbed close to the usual fledging date (21–24 days old). To estimate the influence of rainfall on sex ratio, we recorded rainfall throughout the season.

We captured all birds in each colony with mist nets and ringed them with a metal ring and a unique color combination. Individuals that evaded the mist nets were subsequently caught before dawn using a net with a narrow opening (about 15 cm in diameter) placed over the nest entrance. We took blood samples from breeders and helpers for genetic sex determination. A potential sex difference in dispersal behavior was investigated by using data from a capture-recapture study initiated in 1993 (Covas et al. 2002; M.D. Andersson, unpublished data).

To identify the birds feeding at a given nest and estimate their feeding rates, we conducted 1–2 h of daily observations for 3–6 consecutive days. These observations were made from a hide placed 2–5 m from the colony. Birds generally resumed normal feeding activities within minutes of the observer entering the hide. The birds attending a nest were identified by the color combination of their rings. Feeding rates (number of visits per hour) were recorded when the nestlings were 7–12 days old. Mean feeding rates were calculated for each helper.

Sexing

Sociable weavers are monomorphic to the human eye. Therefore their sex has to be determined using genetic markers. In birds, the female is the heterogametic sex with one W and one Z chromosome while the male has two Z chromosomes. We amplified CHD (chromo-helicase-DNA-binding) genes located on the W and Z sex chromosomes using the P2 and P8 universal primers of Griffiths et al. (1998).

DNA was extracted from blood samples using standard phenol chloroform extraction procedures, or a DNA extraction kit (DNA-zol: Chomczynski et al., 1997). PCRs were carried out in a volume of 10 µl containing 2 µl of DNA, 0.75 µl of 25 mM MgCl$_2$, 1 µl of 10× buffer (10 mM Tris-HCl, 50 mM KCl and 0.1% Triton X-100), 0.5 units of Taq polymerase (Promega), 0.4 µM of each primer, and 75 µM of dNTP. PCRs were performed in a Uno-Thermoblock thermocycler (Biometra) with a program including the following steps: 94°C for 3 min, followed by 30 cycles of 92°C for 30 s, 46°C for 1 min and 72°C for 1 min. Amplified products were resolved on 3% agarose gels stained with ethidium bromide. On the gels, amplified products displayed two bands for heterogametic females and one single band for males.

Statistical methods

Sex ratios are presented as the proportion of males out of the total number of individuals sexed.

Sex-related differences in helping behavior

We calculated the overall sex ratio of helpers and used exact binomial tests (Conover 1980) to check for a possible deviation from parity. We used mixed models (proc MIXED, SAS Institute) to test for potential 'sex- and age-related' differences in the helpers' feeding behavior. The dependent variable was the number of feeding performed in 1 h. Helper type (one-year-old male, one-year-old female and male older than 1 year) was the explanatory variable. Nest and colony were the random factors.

Sex differences in fledgling body sizes

We used a general linear mixed model to look for cryptic sexual dimorphism among fledglings within a same nest and to investigate the effects of group type, rain and colony size on sexual dimorphism. In this analysis, "nest" and "colony" were the random co-variables, and "sex", "sex by group type interaction", "sex by rainfall interaction" and "sex by colony size interaction", the explanatory variables. These analyses were conducted using proc MIXED (SAS Institute) and a backward selection procedure.

Adult sex ratio and sex of immigrant birds

We computed the overall sex ratio of adults, residents and emigrants. We used exact binomial tests to check for a possible deviation from parity.

Sex ratios

Sex ratios were computed on two samples representing sex ratios at day 9 and day 17 (just before fledging). Sex ratio at day 9 constitutes the largest data set and includes all the nestlings alive the day we collected the blood samples. The fledgling sex ratio includes only broods in which at least one young survived until day 17.

In our sample, the clutch size was 3.3±0.108 (mean±SE, n=63). The proportion of eggs that failed to hatch was 0.057, the proportion of hatch chicks that did not survive until day 9 was 0.060, the proportion of deaths between laying and day 9 was 0.11 and the proportion of deaths between laying and fledgling was 0.20. We only sexed the birds present at day 9 and thus do not have data for 21 chicks that did not hatched or died before day 9. In addition we do not have data for 4 chicks where the sexing method failed.

To evaluate the consequences of this problem, we did a worst case scenario where the 25 unsexed birds were assigned the same sex (either male or female). We performed additional analyses on these two hypothetical worst case samples (one with all the missing individuals being males and one with all the missing individual being females).

Sex ratio variation at the population level

On the four samples described above (day 9, day 17 and the two "worst cases"), we performed exact binomial tests to test if the observed overall sex ratio departed from parity.

Sex ratio variation at the individual level

On the four samples described above, we analyzed possible causes for variations in the individual sex ratio using a generalized linear mixed model with binomial error distribution (Krackow and Tkadlec 2001). We used GLIMMIX (SAS Institute) and backward selection procedures. The random co-factors were "nest" and "colony". The following explanatory variables and their ensuing two-way interactions were tested: "group type" (presence versus absence of helper/s), "rainfall" (total rainfall over the 30 days prior to laying date for sex ratio on day 9, and prior to day 17 for fledgling sex ratio), season (1999–2000 or 2000–2001) and "colony size" (total birds captured at each colony).

Number and sex of helpers have been found to be two important sources of variation in nestling sex ratios (Komdeur et al. 1997; Pen and Weissing 2000; Legge et al. 2001). We tested the effect of the number of helpers by running the same analysis as above with the continuous variable "group size" (from 1 to 3 helpers) instead of "group type". It was not possible to test the effect of the sex of helpers because the 29 nests where helpers had been sexed did not contain enough female helpers (female helpers predominated in only 4 nests, compared to 20 nests that contained male helpers only and 5 nests with one male and one female helper).

Results

Sex and age-related differences in helping behavior

Helpers older than one year were invariably males (n=12). First year helpers were predominantly males (26 males versus 13 females), although this difference was not statistically significant (P=0.055, exact binomial test).

Helper type (i.e. one year old males, one year old females and males older than one year) had a significant effect on helper's feeding rate ($F_{2,11}$=4.53, P=0.036; Fig. 1). One-year-old female helpers fed significantly less than older male helpers (contrast analyses: P=0.012). There was no significant difference in the feeding rates of male and female helpers in their first year (contrast analysis P=0.27; Fig. 1) nor between the feeding rates of one year old males and older males (contrast analysis P=0.087; Fig. 1).
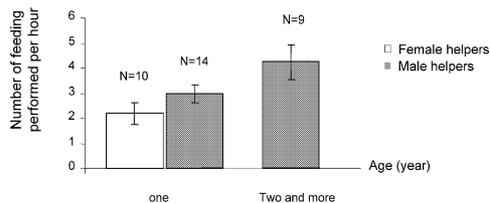
Fig. 1 Mean (±SE) feeding rates of male and female sociable weaver *Philetairus socius* helpers according to their age. The feeding rate is the number of feeding events observed per hour
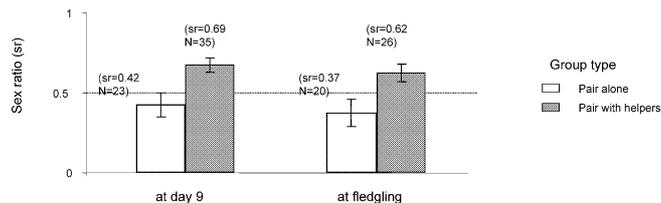

Fig. 2 Sex ratio (*sr*) for broods raised by pairs with and without helpers 9 and 17 days after hatching. The sex ratios are the proportion of males out of the total number of individuals sexed. Data presented are means±SE. Exact values of average sex ratio and sample sizes are given in parentheses over the *bars*
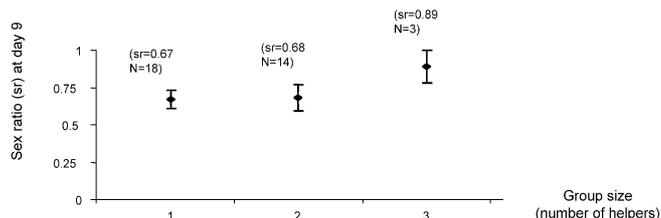

Fig. 3 Sex ratio (proportion of males) of 9-day-old broods according to the number of helpers. Data presented are means±SE. Exact values of average sex ratio and sample sizes are given in parentheses over the *bars*

Sex-related differences in fledgling body size

Within the same nest, male nestlings were slightly but not significantly heavier than females ($F_{1,47}=3.07$, $P=0.08$, mean±SE, $n=71$, mass=29.25±0.344 g for males and 28.4±0.409 g for females) and males had a significantly longer tarsus than females ($F_{1,47}=4.34$, $P=0.04$, mean ±SD, $n=71$, tarsus=23.64±0.105 mm for males and 23.36 ±0.099 mm for females). None of the interactions between sex, group type, rain and colony size was significant.

Adult sex ratios and sex bias in dispersal

The sex ratio of the 243 adults sexed was not biased (0.52:127 males for 116 females, $P=0.52$, exact binomial test). We were able to identify the sex and the natal colony of 68 adults over the age of 2 years. Among these, immigrant birds were predominantly females (29 immigrant females versus 6 males, $P=0.0001$), whereas philopatric birds were mostly males (27 philopatric males versus 6 females, $P=0.0003$).

Nestling sex ratio

Sex ratio at day 9

In the 58 broods where all chicks had been sexed at day 9, the overall sex ratio did not depart significantly from parity (0.57; 97 males out of 170 nestlings, $P=0.077$, exact binomial test).

At the individual level, pairs with helpers produced significantly more males than pairs without helpers ($F_{1,52}=7.24$, $P=0.008$; Fig. 2). The difference in sex ratio of pairs with and without helpers increased though not significantly with colony size and group type (interaction between colony size and group type: $F_{1,82.6}=3.67$, $P=0.059$). The effects of rain, season, colony size and the subsequent interactions were all not significant. When we run the analysis with "group size" instead of "group type", the effect of "group size" (the total number of helpers attending a nest) was not significant ($F_{1,30.1}=0.75$, $P=0.39$; Fig. 3).

Sex ratio at day 17

Between day 9 and day 17, eight broods suffered brood reduction and thirteen broods disappeared completely. Among the eight broods that suffered brood reduction, six females (F) and three males (M) died (4 F and 1 M in nests without helpers, and 2 M and 2 F in nests with helpers). Predation by snakes was likely to be the main cause of disappearance in 10 out of 13 broods where none of the chicks survive either because the presence of snake was observed just before their disappearance, or because several adjacent nests disappeared simultaneously.

For the 46 broods where at least one chick was still alive at day 17, the overall fledgling sex ratio did not depart from parity (0.54, 67 males out of 124 nestlings, $P=0.42$).

As before, there was a significant effect of the "group type" on the pre-fledging sex ratio $F_{1,39.7}=5.57$, $P=0.02$). Pairs with helpers produced significantly more males than pairs alone (Fig. 2). The difference in sex ratio of pairs with and without helpers increased though not significantly with colony size and group type (interaction between colony size and group type: $F_{1,65}=3.18$, $P=0.08$). The effects of rain, season, colony size and the subsequent interactions were not significant. When we run the analysis with "group size" instead of "group type", the effect of "group size" was not significant ($F_{1,67}=0.10$, $P=0.74$).

Worst case sex ratio simulations

If all the dead or non-sexed chicks were males, we would have a primary sex ratio of 0.62 (127 males out of 205 nestlings, $P=0.0008$) and we would have found a significant effect of the presence of helpers on individual sex ratio ($F_{1,52.3}=6.2$, $P=0.016$, with a sex ratio of 0.52 ± 0.300 in nests without helpers and 0.70 ± 0.265 in nests with helpers). None of the other factors tested was significant.

If all the dead or non-sexed chicks were females, we would have a primary sex ratio of 0.50 (102 males out of 205 nestlings) and we would have found a significant effect of the presence of helpers on individual sex ratio ($F_{1,585}=5.4$, $P=0.02$, with a sex ratio of 0.39 ± 0.331 in nests without helpers and 0.59 ± 0.260 in nests with helpers). None of the other factors tested was significant.

Discussion

In this study, we found that males help more and disperse less often than females and that pairs with helpers produce more males than pairs without helpers. No consistent bias was detected in overall sex ratio. This difference in sex allocation between pairs with and without helpers is present 9 days after hatching and just before fledging. It is probably not caused by differential mortality since it was already present in the primary sex ratio when we assigned the same sex to all unsexed chicks and since, the death of male and female nestlings between day 9 and fledgling seems to occur independently of the presence of helpers.

The results presented here are in the direction opposite to the predicted by the helper repayment hypothesis. This hypothesis predicts: (1) an overall sex ratio bias towards the helping sex at the population level; and/or 2) an overproduction of the helping sex by pairs without helpers at the individual level in order to generate helpers. In contrast to these predictions, we found that: (1) the overall adult and nestling sex ratios were not significantly biased towards the helping sex (e.g. the male); and (2), more importantly, it was pairs with helpers that produced additional males, not pairs without helpers.

The differences between our results and the predictions of the helper repayment hypothesis do not seem to be due to departures from the two basic assumptions of this hypothesis, viz. a sex bias in helping behavior and the relatedness between helpers and parents. In our population, males showed a greater tendency than females to help; in another population in Namibia, only male helpers were recorded (Marsden 1999; 15 trios observed). Hence, it seems that in, this species, helpers are predominantly males. Moreover we found that helpers increased: (1) nestling survival (Covas et al., unpublished data); (2) fledgling mass when the external conditions were bad (low rainfall: Covas et al., unpublished data); and (3) fledgling success when the brood size is artificially increased (Covas et al., unpublished data). Microsatellite analyses suggest that 1-year-old helpers are always the offspring of at least one parent ($n=35$; Doutrelant et al., unpublished data) whereas 2-year-old male helpers may be unrelated ($n=6$ unrelated and 3 related; Doutrelant et al., unpublished data). Thus, sociable weavers can theoretically repay the cost of their own production for at least one season and we could therefore have expected a sex ratio bias toward males.

Why do sociable weavers produce more males when they have helpers? A bias towards the more costly sex when conditions are good could be an alternative explanation if, for undetected reasons, sons are more costly to produce or if one considers that the sex-related difference we found in tarsus length indicates that males are more costly to produce. Conditions could be improved by the presence of helpers as nests with helpers feed slightly more than nests without helpers (Covas and Doutrelant, unpublished data). Conditions could also be increased if one or both parents have better raising abilities. Superior parents may have a higher reproductive success and hence have a higher probability of obtaining helpers. However, we did not detect any significant sex-related difference in fledgling weight and we did not find any significant effect of rainfall, a factor which has been shown to dramatically affect sociable weavers' breeding performance (Covas 2002; Covas et al., unpublished data; Maclean 1973b) and that could have been favorable to the production of the more costly sex.

Another possible explanation for the results presented here is that the overproduction of males in nests with helpers is linked to the quality of one or both parents. In this case, the presence of helpers would be a confounding factor (high quality parent(s) would produce more sons and would have a higher probability of gaining helpers). The skew towards production of males by good quality pairs could take place if: (1) good quality pairs, having a high rank in the dominance hierarchy of the colony, produce more males because their sons are more likely to obtain a breeding position in the colony due to their protection/dominance or to the inheritance of the high quality traits favoring future dominance; or (2) male quality could play a role if females paired with good genetic quality males overproduce sons to pass the good quality traits of their father (e.g., Burley 1981; Sheldon et al. 1999). Although similar hypotheses have received support from studies of non-cooperative species, we are unaware of any study of these possibilities in a cooperative breeder. This could be tested for example by altering the condition or the dominance of the pairs, by removing helpers or by altering the apparent male quality. Ongoing studies will be investigating the role of parental quality on offspring sex ratio in this species.

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