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Adult sex ratios and their implications for cooperative breeding in birds

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Cooperative breeding is a form of breeding system where in addition to a core breeding pair, one or more usually non-breeding individuals provide offspring care. Cooperative breeding is widespread in birds, but its origin and maintenance in contemporary populations are debated. Although deviations in adult sex ratio (ASR, the proportion of males in the adult population) have been hypothesized to influence the occurrence of cooperative breeding because of the resulting surplus of one sex and limited availability of breeding partners, this hypothesis has not been tested across a wide range of taxa. By using data from 188 bird species and phylogenetically controlled analyses, we show that cooperatively breeding species have more male-biased ASRs than non-cooperative species. Importantly, ASR predicts helper sex ratio: in species with more male-biased ASR, helper sex ratio is also more male biased. We also show that offspring sex ratios do not predict ASRs, so that the skewed ASRs emerge during the period when individuals aim to obtain a breeding position or later during adulthood. In line with this result, we found that ASR (among both cooperatively and non-cooperatively breeding species) is inversely related to sex bias in dispersal distance, suggesting that the cost of dispersal is more severe for the further-dispersing sex. As females usually disperse further in birds, this explains the generally male-biased ASR, and in combination with benefits of philopatry for males, this probably explains why ASR is more biased in cooperatively breeding species. Taken together, our results suggest that a sex bias in helping in cooperatively breeding species relates to biased ASRs. We propose that this relationship is driven by sex-specific costs and benefits of dispersal and helping, as well as other demographic factors. Future phylogenetic comparative and experimental work is needed to establish how this relationship emerges.

This article is part of the themed issue 'Adult sex ratios and reproductive decisions: a critical re-examination of sex differences in human and animal societies'.

1. Introduction

Across cooperatively breeding species, a core breeding pair is often assisted in offspring care by subordinate individuals that often do not reproduce themselves [1–3]. While the benefits to those receiving assistance are often clear, the question remains as to why individuals would delay their own reproduction in order to help others [2]. Several hypotheses have been proposed with the aim to understand how a suite of social, genetic and ecological factors promote the evolution and maintenance of these behaviours [1,3,4].

Ecological constraints, like habitat saturation or shortage of potential partners resulting in a lack of breeding opportunities for maturing individuals, have been important in explaining why some individuals either delay or completely forgo independent reproduction [2,5–9]. If this is the case, individuals may delay dispersal and stay in a group as non-reproductive (or sometimes

as co-breeding helpers) [9–14] while waiting until a vacancy or a partner becomes available. Philopatry may improve individuals' survival probability compared to survival of individuals who leave to search for no or limited opportunities for independent reproduction [14–15]. For example, nepotism by parents may facilitate access to food [13,16,17] and thus improve survival, which can be a major benefit in light of the severe competition outside a resident territory that might lead to reduced food intake and increased mortality risk [14,15].

We hypothesize that if dispersal is indeed costly, a sex bias in dispersal in cooperative breeders may lead to a shortage of individuals of the dispersing sex, which in turn could lead to philopatry of the other sex. In many bird species, dispersal is biased towards females, as females usually disperse further (or earlier) in life to attempt to obtain a breeding territory or position [18–23]. Dispersing individuals in most cooperatively breeding species may face severe competition while finding a place to settle because availability of territories or partners may be limited [3,7,8], and in such species, dispersal costs may therefore be especially high. Thus, if dispersal is sex-biased, this may lead to sex-biased mortality and biased adult sex ratios (ASRs; usually expressed as the proportion of males in the adult population). As limited partner availability (in addition or alternatively to shortage of breeding territories) can lead to delayed dispersal by the surplus sex, this may ultimately lead to group formation and thus facilitate cooperative breeding, polygyny or polyandry.

Several empirical studies support this 'ASR-cooperation hypothesis'. In the Galápagos mockingbird (*Nesomimus parvulus*) males refrained from breeding in years when the ASR was male-biased, and many males became helpers instead, whereas in years with female-biased ASR, polygynous groups formed [24]. Similarly, in superb fairy-wrens (*Malurus cyaneus* [25]) and pygmy nuthatches (*Sitta pygmaea* [26]) a shortage of females, rather than habitat saturation *per se*, appeared to drive males to become helpers. Even for obligate cooperative breeders, where breeding without help is uncommon and seldom successful, a bias in ASR reflecting a potential shortage of one sex may be an important determinant of biases in the helper sex ratio. For example, obligate cooperatively breeding miner species (*Manorina* spp.) have many helpers, but nearly all are male [27,28]. However, apart from some single-species studies and despite earlier notions that ASR may promote cooperative breeding [29,30], the broad relevance of ASR bias for cooperative breeding remains untested. This is a key point given that dispersal limitations and resultant group formations are not only due to territory/food resource limitations but may also be promoted by partner shortage.

ASR bias may also lead to increasing intra-sexual competition. The ASR is a key factor for understanding evolution under sexual selection [31,32]. Recent theoretical, experimental and phylogenetic studies have drawn attention to reproductive strategies in response to partner availability and to the significance of the social environment [33–35]. Because the number of males and females in a population structures both individual reproductive options and interactions between those of the same and opposite sex, the ASR has been increasingly recognized as a demographic variable driving behavioural variability within and between the sexes [32,36]. For example, if males outnumber females, both male courtship behaviour and male–male competition intensify [37–39]. Moreover, at male-biased ASR, males are less likely to search

for additional mates and are more likely to provide care for their young than at female-biased ASRs [40–42]. These phenomena therefore potentially point to a link between ASR bias and social behaviour that may include cooperative breeding. Despite the potential importance of ASR for breeding system evolution, most research on the evolutionary ecology of sex ratios has focused on operational sex ratios (OSR; usually expressed as the proportion of reproductive males in the adult reproductive population [34]). Note that OSR and ASR provide complementary information about populations [36,43], and temporal variation in ASR were independent from those in OSR in birds and mammals [44,45]. Here we focus on ASR because it is a product of demographic processes, such as sex-biased dispersal, mortality and partner availability (and thus includes helpers and floaters), whereas OSR is restricted by reproductive decisions of individuals [34,36].

For the present analyses, we use data from 156 non-cooperatively and 32 cooperatively breeding bird species to test the ASR-cooperation hypothesis. Specifically, we tested the predictions that (i) sex-biased dispersal relates to biased ASR across birds (including cooperatively and non-cooperatively breeding species), while assessing whether biased offspring sex ratio cannot alternatively explain biased ASRs, (ii) ASR is more biased in cooperatively breeding species, and (iii) biased ASR predicts the helper sex ratio (the proportion of helpers that are males).

2. Material and methods

(a) Data compilation

We augmented the ASR data based on an intensive literature survey presented in a recent study [36] by adding four additional species (see below). ASR is calculated as the proportion of adult males present in the population (i.e. the number of adult males/ number of adult males and number of adult females; for details on collection of ASR data, see [36]). Adults included are all post-maturation individuals regardless of their reproductive stage or status (i.e. breeder or non-breeder, floater or sexually mature helper). ASRs are estimated in a variety of ways [43], but for birds ASR estimates appear to be reliable because (i) they are highly repeatable between studies on the same species [43], (ii) for most species (80%), the direction of ASR bias was the same for all repeated estimates [36,43], and (iii) intraspecific variation in ASR was independent of sample size, suggesting that ASRs are not biased by sampling effort [36]. One species included in [36], the snowy plover (*Charadrius nivosus*), was not included in our comparative study, because it was not included in the phylogeny (see below).

We classified each species as cooperative or non-cooperative breeder based on the classification in [46]; broadly defined, cooperative breeders are species in which more than the core breeding pair may raise the offspring. As in some species only some populations breed cooperatively, we checked the primary literature to confirm that all the compiled data for the 39 species listed as cooperative breeders in [46], including ASR values, originate from populations with cooperative breeding. This way, we redefined seven of these species as 'non-cooperative' because either data were obtained from a non-cooperatively breeding population (carrion crow (*Corvus corone*), Australian magpie (*Gymnorhina tibicen*), house sparrow (*Passer domesticus*), Eurasian oystercatcher (*Haematopus ostralegus*), common kiwi (*Apteryx australis*) and peregrine falcon (*Falco peregrinus*)) or because these were species in which females of polygynous males built separate nests (lesser spotted woodpecker (*Dendrocopos minor*) and
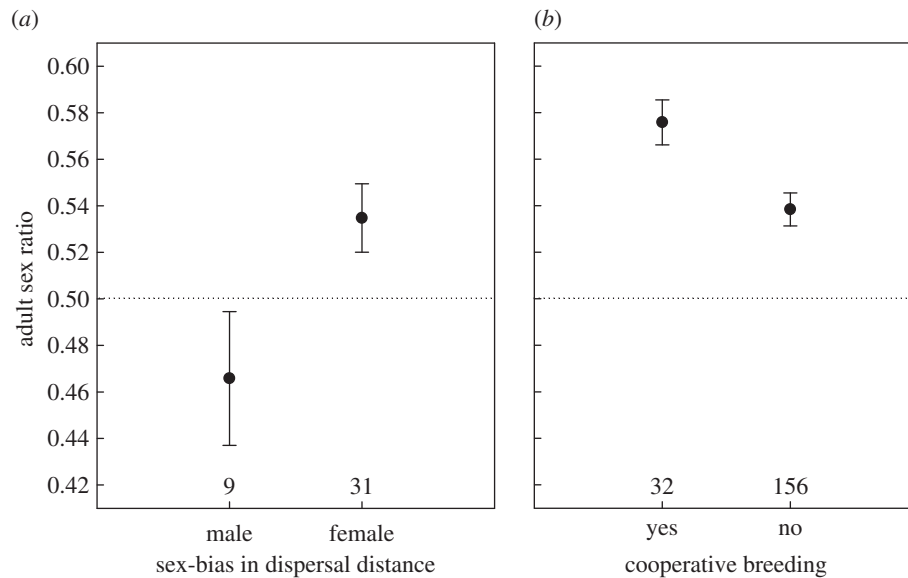
Figure 1. Adult sex ratio (proportion of males in the population) is more male-biased in bird species (*a*) with female-biased dispersal and (*b*) in cooperatively breeding bird species. Mean ($\pm$ s.e.) adult sex ratio is given in relation to (*a*) sex bias in dispersal in birds (cooperatively and non-cooperatively breeding species combined), and (*b*) whether species breed cooperatively or not. Numbers indicate the number of species. Tests statistics are provided in table 1.

bobolink (*Dolichonyx oryzivorus*)) (see electronic supplementary material, appendix S1 for references). For the remaining 32 cooperatively breeding species, the ASR data were obtained from populations where cooperative breeding (as defined above) occurs. In addition to ASR, we also attempted to collect data for each species on offspring (hatching and fledging) sex ratios, helper sex ratios and sex-biased dispersal.

Hatching sex ratios and fledgling sex ratios (proportion of males of freshly hatched chicks and fledged young, respectively) were collected from [22,36], and we augmented these datasets by an extensive search in the primary literature with offspring sex ratios for two species: splendid fairy wren (*Malurus splendens* [47]) and apostlebird (*Struthidea cinerea* [48]). The majority of offspring sex ratios (at hatching and fledging) were obtained using molecular methods and few were based on sex-specific morphological differences [22,36].

Helper sex ratio data were obtained from Komdeur [22]. For four cooperatively breeding species with known helper sex ratios listed in [49], we were able to retrieve data on ASR by searching the Web of Science and Google Scholar using keywords 'cooperative breeding' and the scientific names of specific taxa: Karoo scrub-robin (*Erythropygia coryphaeus* [50]), red-cockaded woodpecker (*Picoides borealis* [51]), rifleman (*Acanthisitta chloris* [52]) and western bluebird (*Sialia mexicana* [53]).

Sex-biased dispersal was defined by whether one sex dispersed on average further from their site of origin than the other, based on individually recaptured/marked males and females (data provided in [23,54]).

The complete data (including 156 non-cooperative and 32 cooperatively breeding species) with full references are available in the electronic supplementary material, appendix S1.

(b) Statistical analyses

To address the three predictions of the ASR-cooperation hypothesis (see above), we carried out three main analyses using R v. 3.3.0 [55]. We controlled for phylogenetic dependence including the avian phylogeny (using maximum-likelihood estimation of λ) in one-sample *t*-tests or phylogenetic least-square (PGLS) models using the caper package [56]. To test whether sex ratios deviated from parity, we obtained estimates of average sex ratio by running PGLS models without any explanatory variables and sex ratio as the response variable. We evaluated whether these

estimates (the intercept of the models) were different from 0.5 using one-sample *t*-tests based on the mean, standard error and sample size. We repeated each test using 100 trees (with the Hackett backbone), downloaded from http://birdtree.org [57], and report the average values of these tests. For all analyses, model residuals were normally distributed.

First, we tested whether ASR (response variable) differed between species (cooperatively breeding and non-cooperatively breeding species combined) that had female-biased dispersal (i.e. females dispersed further than males) or male-biased dispersal (using PGLS). In addition, we tested whether ASR differed from parity for species with either female- or male-biased dispersal. One species, the non-cooperatively breeding whinchat (*Saxicola rubetra*), which had equal male and female dispersal [58], was excluded from the latter analysis.

Second, we tested whether hatching sex ratio, fledging sex ratio and ASR differed from parity (in all species, and also for cooperatively and non-cooperatively breeding species separately), and tested whether these differed between species that breed cooperatively and those that do not (using PGLS). For the analyses including fledgling sex ratio, we excluded two non-cooperatively breeding species with exceptionally male-biased fledgling sex ratio (Kentish plover (*Charadrius alexandrines*) and zebra finch (*Taeniopygia guttata*); see the electronic supplementary material, appendix S1).

Third, we tested whether helper sex ratio differed from parity, and we analysed whether helper sex ratio (proportion of helpers that are males as dependent variable) was associated with ASR (as predictor), and whether helper sex ratio predicted hatching and fledging sex ratio (because females may adjust offspring sex ratio to produce offspring of the helping sex).

3. Results

(a) Sex-biased dispersal and adult sex ratio

Consistent with previous studies [18–20,23], dispersal distance was female-biased in most species in our dataset (73.2%, 31 species out of 41 species). In species with female-biased dispersal, ASR was significantly more male-biased than in species with male-biased dispersal ($t = 2.201$, $n = 40$ species, $p = 0.034$; figure 1*a*). In species where females dispersed further

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Table 1. Hatching, fledging, helper and ASRs in birds, and whether these deviated significantly from parity for (a) all included species, (b) non-cooperatively and (c) cooperatively breeding bird species. Means are based on raw data, whereas the test statistics were controlled for phylogeny. n refers to the number of species.

	mean ± s.e.	n	t	p
(a) all species			deviating from parity?	
hatching sex ratio	0.518 ± 0.006	56	3.154	0.003
fledgling sex ratio[a]	0.501 ± 0.005	51	0.257	0.798
adult sex ratio	0.545 ± 0.006	188	4.031	<0.001
(b) non-cooperative breeders				
hatching sex ratio	0.515 ± 0.006	44	2.272	0.028
fledgling sex ratio	0.498 ± 0.006	38	0.473	0.639
adult sex ratio	0.538 ± 0.007	156	5.429	<0.001
(c) cooperative breeders				
hatching sex ratio	0.528 ± 0.011	12	2.573	0.026
fledgling sex ratio	0.510 ± 0.011	13	0.879	0.397
helper sex ratio	0.844 ± 0.034	32	2.895	0.007
adult sex ratio	0.576 ± 0.010	32	7.865	<0.001

[a]Excluding two species with exceptionally male-biased fledgling sex ratio (Kentish plover and zebra finch; see Material and methods).

Table 2. The relationships between hatching sex ratios, fledging sex ratios and adult sex ratio (response variable) in (a) all species, (b) non-cooperatively, and (c) cooperatively breeding bird species. Estimates are based on statistical tests controlling for phylogeny (PGLS models). n refers to the number of species.

	slope ± s.e.	n	t	p
(a) all species				
hatching sex ratio	0.421 ± 0.290	56	1.455	0.155
fledgling sex ratio	0.568 ± 0.342	51	1.662	0.103
(b) Non-cooperative breeders				
hatching sex ratio	0.261 ± 0.342	44	0.764	0.456
fledgling sex ratio	0.549 ± 0.400	38	1.373	0.178
(c) cooperative breeders				
hatching sex ratio	−0.177 ± 0.347	12	−0.514	0.623
fledgling sex ratio	0.269 ± 0.398	13	0.677	0.513

than males, ASR was significantly male-biased (figure 1a; mean ASR = 0.535; one-sample t-test: $t = 2.361$, $n = 31$ species, $p = 0.025$), whereas in species with male-biased dispersal, ASR was female-biased (figure 1a; mean ASR = 0.466), although not significantly different from parity perhaps due to limited statistical power (one-sample t-test: $t = 1.188$, $n = 9$ species, $p = 0.269$).

All cooperatively breeding species with known dispersal bias had female-biased dispersal (100%; $n = 6$), whereas of the 35 non-cooperatively breeding species, only 71.4% had female-biased dispersal ($n = 25$ species; nine species had male-biased dispersal and in one species males and females dispersed on average equal distances).

(b) Adult, helper and offspring sex ratio
The average ASR was male-biased and deviated significantly from parity in all species (mean = 0.545; table 1a), and in both cooperatively (mean: 0.576; table 1b) and non-cooperatively breeding species (mean = 0.538; table 1c). In cooperatively breeding species, the ASR was significantly more male-biased compared to non-cooperatively breeding species ($t = 2.290$, $p = 0.023$; table 1 and figure 1b).

Hatching sex ratio was slightly, but significantly, male-biased (mean = 0.518) when including all species, and also for non-cooperatively (mean = 0.515) and cooperatively (mean = 0.528) breeding species separately (table 1). However, fledgling sex ratio did not significantly differ from parity for all species combined, and for non-cooperatively and cooperatively breeding species separately (table 1). Both hatching and fledgling sex ratio did not differ between cooperatively

and non-cooperatively breeding species ($t = 1.020$, $p = 0.312$ and $t = 0.924$, $p = 0.360$, respectively; table 1).

ASR was not predicted by either hatching or fledging sex ratio in all species (table 2a), or in only non-cooperatively (table 2b) or cooperatively breeding species (table 2c).

(c) Helper sex ratio
Helper sex ratio varied widely among cooperatively breeding bird species (range = 0.430–1.000), but was on average male-biased and differed significantly from parity (mean = 0.844; table 1). ASR predicted helper sex ratio because species with male-biased ASR also exhibited male-biased helper sex ratio ($n = 31$ species, $t = 3.45$, $p = 0.002$; figure 2). The difference between helper sex ratio and ASR was higher with strongly male-biased ASR values (PGLS, slope = 1.940 ± 0.563 (s.e.); figure 2), but the slope of the regression was not significant from 1 as it was included in the 95% CIs of the slope (95% CI's: 0.811–3.138).

Helper sex ratio was not associated with hatching sex ratio (PGLS, slope = 0.042 ± 0.057, $n = 12$ species, $t = 0.750$, $p = 0.471$) nor fledgling sex ratio (PGLS, slope = -0.004 ± 0.061, $n = 13$ species, $t = 0.063$, $p = 0.951$), suggesting that females do not adjust the sex of their offspring to the helping sex and that offspring sex ratio did not predict helper sex ratio.

4. Discussion
In cooperatively breeding species, subordinate individuals delay independent reproduction. Although this strategy is often attributed to habitat saturation, one additional factor that may play a role is a biased ASR (which may indirectly be caused by habitat saturation), leading to a shortage of one sex for all individuals of the opposite sex to reproduce independently. In line with predictions of this ASR-cooperation hypothesis, our results show that ASR is (i) related to sex bias in dispersal across birds, (ii) more male-biased in cooperatively breeding species compared to non-cooperatively breeding species, and (iii) positively related to helper sex ratio. We discuss these and other proximate and ultimate components of ASR variation below, specifically highlighting the implication of ASR bias for the evolution of cooperative breeding.
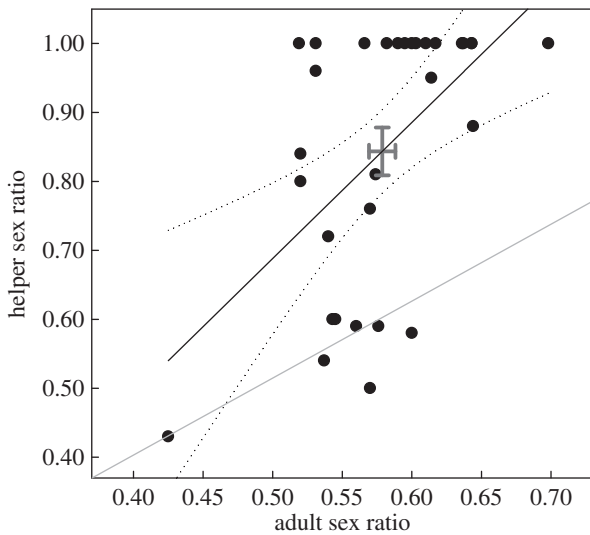
Figure 2. Adult sex ratio (proportion of males in the population) in cooperatively breeding bird species predicts helper sex ratio (proportion helpers that is male). Dots show species values. Mean ($\pm$ s.e.) adult sex ratio and helper sex ratio are shown using a bi-directional error bar in grey. Dashed lines depict 95% confidence intervals. The grey line provides the 1 : 1 relationship between ASR and helper sex ratio. Tests statistics are provided in the main text.

(a) Association between adult sex ratio, sex-biased dispersal and cooperative breeding

In birds, dispersal is often female-biased, and our results confirm this sex difference. We found that females often disperse further than males, regardless whether a species is a cooperative breeder or not. As ASR is male-biased in species with female-biased dispersal, and in species with male-biased dispersal ASR tends to be female-biased (figure 1a), this result suggests that dispersal is costly, as shown in several birds species previously ([18], reviewed in [59]). That the biases in ASR are likely a consequence of costs of dispersal is also supported by our finding that offspring sex ratio, although slightly male-biased overall, does not predict ASR consistently ([36]; our study). Apart from the fact that dispersal costs may be sex-specific in the first place [60,61], one reason for such sex-biased costs for the further-dispersing sex may be due to, for example, competition with conspecifics and enhanced predation risk [59].

Our second result, that the ASR is more male-biased in cooperatively breeding species, suggests that the dispersal costs are relatively more severe for females in cooperatively breeding species. This is perhaps not surprising for two reasons: first, in cooperative breeders, saturated habitat makes it difficult for individuals to find an independent breeding position once they have left the natal territory and competition is severe. Second, the relatively more philopatric sex (i.e. males) may avoid the costs of dispersal by staying in a 'safe-haven' of the resident territory [14]. In such cases, males may wait in a territory to either inherit the territory when a same-sex breeder dies or they wait for a breeding vacancy to appear nearby. For example, subordinate male Seychelles warblers often shift to a nearby territory to breed, whereas females are more likely to float and search for a breeding vacancy further away [14]. Females may disperse, for example, because they were evicted from the group due to reproductive competition when they remain in a group.

In cooperatively breeding species, females can be very competitive over reproduction within groups and eviction often appears to be driven by conflict over reproduction. For example, in groove-billed anis (*Crotophaga sulcirostris* [62]) and guira cuckoos (*Guira guira* [63]), where groups can comprise multiple females breeding in communal nests, nest abandonment is relatively common because all of the eggs are tossed out or all nestlings are killed. To avoid this outcome and to maintain their reproductive monopoly, dominant females may evict reproductive competitors from the group. In meerkats (*Suricata suricatta* [64]) and banded mongoose (*Mungus mungo* [65]), dominant females evict subordinate females from their group to prevent infanticide attacks on their pups. Subordinates that are evicted were shown to experience a deterioration in condition, higher levels of stress and lower survival [66]. Alternatively, females may disperse to avoid inbreeding [18]. For example, in purple-crowned fairy-wrens (*Malurus coronatus* [67]) and acorn woodpeckers (*Melanerpes formicivorus* [68]), female divorce and dispersal is driven by inbreeding avoidance, creating opportunities for subordinate females to disperse from their group to fill such a dominant breeding position. This high skew in ASR in cooperative breeders supports the prediction that a larger bias in the population sex ratio may predispose the individuals from the overrepresented sex to stay in the natal territory. This may in turn result in a biased helper sex ratio.

Interestingly, sex-biased dispersal may be self-reinforcing: if females become the limiting sex as partners or if males are the surplus sex, searching or successfully competing for a vacancy may become more costly for males, so that such males have nowhere to go and delay dispersal even more, whereas dispersal becomes more costly for females. This prediction is supported by our third result that across cooperatively breeding species, helper sex ratio is on average strongly male-biased and that helper sex ratio is positively associated with ASR (figure 2), but not with hatching sex ratio. Furthermore, with increasingly male-biased ASR the helper sex ratio tends to become even more male-biased (figure 2). Therefore, our results suggest that ASR is associated with cooperative breeding across bird species, confirming long-standing predictions [29,30]. Nonetheless, the association between ASR and helper sex ratio may be relevant beyond birds, and we encourage researchers working on mammalian systems to test whether the ASR and helper sex ratio relationship applies to mammals also.

(b) Adult sex ratio bias and the evolution of cooperative breeding

Male-biased ASR can either be a cause or a consequence of sex-biased helping, but regardless of the causal relationship, it is clear that a male-biased ASR is associated with a male bias in helping behaviour. It appears that the stronger the ASR bias is, the higher the bias tends to be in helping behaviour towards males. In some species, a bias in ASR corresponds to a similar sex bias among helpers. For example, the ASR corresponds to an almost identical sex ratio of helpers in acorn woodpeckers, where the mean sex ratio of breeders in the population was 58.1%, whereas the mean sex ratio of helpers was almost identical (57.7%) across 33 years of research [2]. Interestingly, in cooperative mammals, dispersal is often male-biased, and females generally form the surplus sex and are more likely to help than males. This

difference between birds and mammals may be due to better opportunities for subordinate females to breed in mammals compared to birds, who have to compete for a space in the nest to lay an egg [69].

The biased sex ratio of helpers is not always directly related to ASR bias and a link between them might not be causative, for example, because helper sex ratio may be determined by biased offspring sex ratio, or be due to sex-specific differences in ultimate benefits of helping. First, in some species, males as well as females are constrained by independent breeding, resulting in groups with male and female helpers, and, in others, help may be independent of ASR bias. For example, in long-tailed tits (*Aegithalos caudatus*) the population sex ratio is at parity, but nonetheless there is a strong tendency for helpers to be males (84%; [70]). The fact that in this species mainly males help nearby breeders after their own brood fails suggests that other factors may explain sex-biased helping in this, but potentially also in other species (for example, limited dispersal and kin-clustering may cause males to easily direct help to relatives). Second, our analyses show that across birds (in both cooperatively and non-cooperatively breeding species) neither hatching nor fledging sex ratios predict ASR, and for cooperatively breeding species hatching sex ratios neither predict ASR nor helping sex ratios (cf. [71]), suggesting that ASR bias is not caused by adaptive sex allocation in cooperative breeders. Third, differential benefits of delayed dispersal may drive sex-biased helping and philopatry. For example, although helpers do not obtain parentage in many cooperative breeders, the biased sex ratio of helpers may also be partly due to a potentially higher probability of gaining parentage for males than females. For example, a male's help may be correlated with his probability of gaining paternity, simply achieved through copulations with a breeding female, whereas egg laying by subordinate females may be more difficult to achieve. A breeding female may actively enlist help from males by distributing her copulations among males in a group, but actively avoid competition from reproducing female subordinates, which will then have lower propensity to help [72].

(c) Conclusions and recommendations for future research

Overall, the differential costs and benefits of dispersal and helping may lead to biased helper sex ratios, which, in turn, reinforce the costs of dispersal, for example, through causing more intense competition for breeding vacancies. Currently, we cannot exclude the possibility that the association between ASR and helper sex ratio is due to sampling bias: if population-level sex ratios were based on sex ratios of only individuals in groups (thus excluding non-observed adults not present in the group; e.g. floaters), and may result in wrong ASR estimates, then the association may emerge due to sampling design. However, we believe this is unlikely because ASR estimates

were usually based on population-level censuses including floaters and/or surveys during the non-breeding season. In summary, the evolution of cooperative breeding in birds and other taxa is perhaps driven by a complex interplay between biases in costs of dispersal, costs and benefits of helping and other sex-biased demographic factors that may cause one sex to become limited.

Our analyses are correlative in nature and the studies included in this review were non-experimental, and it is therefore difficult to disentangle cause and consequence. The importance of ASR for cooperative breeding should therefore be further investigated by controlling for benefits such as kin selection, nepotism and environmental factors that drive selection on delayed dispersal and cooperation. The role of ASR in cooperation can best be investigated in facultative cooperatively breeding species (not for cooperatively breeding species with redirected care or species with very strong habitat saturation), and in species in which the benefits of staying and helping do not greatly differ between males and females. In order to demonstrate causal relationships between ASR and cooperative breeding, it is necessary to carry out experimental manipulations of ASR [25,32]. Studies on cooperatively breeding species that did manipulate ASR at the population level directly and investigated the responses in terms of cooperative care of individuals to altered ASR have not been conducted in the wild. If supported by follow-up studies, the 'ASR-cooperation hypothesis' would have important implications for understanding cooperative breeding systems. Sex differences in survival of helpers and non-helpers can be either a cause [73,74] or a consequence of cooperative breeding [75], and to separate these explanations it would be interesting to manipulate helper sex ratio, ASR or both in population studies.

In conclusion, our work suggests that cooperative breeding is associated with ASR in birds, supporting the predictions of the ASR-cooperation hypothesis. Although the precise mechanism driving this relationship requires further analyses, and data quality and sampling methodologies will need to be refined and/or extended [43]), our phylogenetic analyses suggest that ASR not only relates to mating systems and parental care in birds, but also to cooperative breeding.

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