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Hard-working helpers contribute to long breeder lifespans in cooperative birds

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In many species that raise young in cooperative groups, breeders live an exceptionally long time despite high investment in offspring production. How is this possible given the expected trade-off between survival and reproduction? One possibility is that breeders extend their lifespans by outsourcing parental care to non-reproductive group members. Having help lightens breeder workloads and the energy that is saved can be allocated to survival instead. We tested this hypothesis using phylogenetic meta-analysis across 23 cooperatively breeding bird species. We found that breeders with helpers had higher rates of annual survival than those without helpers (8% on average). Increased breeder survival was correlated with reduced investment in feeding offspring, which in turn depended on the proportion of feeding provided by helpers. Helpers had similar effects on female and male breeder survival. Our results indicate that one of the secrets to a long life is reduced investment in parental care. This appears to be a unique feature of cooperative societies with hard-working helpers.

This article is part of the theme issue 'Ageing and sociality: why, when and how does sociality change ageing patterns?'

1. Introduction

Reproduction is costly. Sexually reproducing species have to find a suitable mate, females often invest a lot of energy in developing embryos and, in some species, offspring require substantial amounts of parental care before reaching independence [1–5]. The energetic costs of reproduction are predicted to be traded-off against somatic maintenance, leading to reductions in survival [6,7]. Consistent with this idea, across a wide range of species, high investment in reproduction has been shown to limit survival [8,9]. This is often not the case, however, in species that raise young in cooperative groups [10,11]. Breeders often live a very long time despite producing many offspring that require substantial amounts of parental care. For example, ant queens live 100 times longer than expected given their body mass but can produce millions of eggs over their lifetimes [10,12]; breeders in *Fukomys* mole-rats live twice as long as non-reproductive group members [13]; and breeding bicolored wrens with helpers have a 13% higher annual survival probability than breeders without helpers yet raise three times as many young [14,15]. How do breeders in cooperative groups escape the trade-off between survival and reproduction and prolong their lifespans?

Breeders in cooperative species may live longer because they outsource parental care to non-reproductive group members [16–18]. This allows them to avoid a large fraction of the costs of reproduction. The more parental care provided by helpers, the less breeders have to invest in offspring, allowing resources to be allocated to processes that promote survival instead. Additionally, if female and male breeders adjust their workloads differently when helped, this could lead to sex-specific survival benefits [19–21]. For example, in pygmy nuthatches, only females reduce their workloads in the presence of helpers [22]. Sex differences in survival may also result from females paying the additional costs of egg production, if these are non-trivial compared with

Figure 1. Facultative cooperative breeders provide an opportunity to test the effect of load-lightening on breeder survival as breeders with and without helpers in the same populations can be compared. The presence of helpers can have a large effect on breeder survival, for example, in the purple-crowned fairy-wren [33] (*a*) or a limited effect on breeder survival, as in the Seychelles warbler [34] (*b*). Helpers may provide a lot of care, as in rufous treecreepers (*c*), which can reduce the amount of care provided by breeders [35]. Alternatively, in the Karoo scrub-robin (*d*), helpers have little effect on breeder workloads, despite investing a comparable amount to breeders in offspring care [36]. We have used the following images from the Macaulay Library at the Cornell Lab of Ornithology: ML76482571, ML193642671, ML257993281, ML252195471.

the costs of parental care. The general extent of sex-specific survival benefits across species remains to be quantified.

Most evidence concerning the effect of helpers on breeder lifespans comes from studies correlating breeder survival with group size, and the results are mixed. For example, breeders live longer in larger groups in tropical hover wasps [23] and red-cockaded woodpeckers [24], whereas in Karoo scrub-robins there is no effect of group size on survival [25]. Larger groups can even decrease breeder survival, as found in African wild dogs [26] and green woodhoopoes [27]. One explanation for these conflicting results is that group size is a poor proxy for breeder and helper investment in parental care. There is considerable variation among cooperative species in how hard helpers work [28–31], and we only expect increased breeder survival in species where helpers take over a large share of parental care, allowing breeders to reduce their workloads. Alternatively, a consistent effect of helpers on breeder survival may simply not exist. In species where helpers cause large reductions in breeder workloads, breeders might invest saved energy in current reproduction (more offspring) rather than survival. It is also possible that in species where helpers do not lighten breeder workloads, correlations between breeder survival and the presence of helpers arise because group-living decreases predation [10,32]. Consequently, whether the care provided by helpers increases breeder lifespans in cooperative species is unclear.

Here, we combine measurements of the effect of helpers on breeder survival with data on breeder and helper workloads to test if the extended lifespans of breeders result from helpers reducing the costs of parental care. We focus

on facultative cooperatively breeding birds (figure 1) because there are a large number of well-studied species in this clade [37,38], breeders are known to produce more offspring when helpers are present [39], so reduced fecundity cannot explain why breeders are long-lived, and parental care has been measured in a consistent way across species (feeding offspring). Specifically, we use phylogenetic meta-analysis to ask if: (*a*) breeders with helpers have a higher probability of surviving between years than those without; (*b*) if the change in breeder survival when helped depends on how much breeders invest in care, and (*c*) if the amount that breeders reduce their care depends on the amount of care helpers provide. We examine the general effects of helpers on breeders by pooling data across the sexes, as well as examining females and males separately to quantify the extent of sex-specific survival benefits across species.

2. Methods

(a) Data collection

To test whether increased breeder survival depends on helpers moderating the costs of parental care, we collected data on: (i) female and male breeder survival probabilities when breeding with and without helpers; (ii) the care provided by female and male breeders with and without helpers, and (iii) the total contribution made by helpers to offspring care. To identify studies containing relevant data, we first compiled a list of cooperatively breeding bird species. We started with the species listed in [39] and updated this to include any newly recognized cooperative

breeders. These were identified by searching Web of Science and Scopus using the search term 'cooperative breeding' (for studies published since 2019). This search returned 163 and 178 studies, respectively, from which we identified four new cooperative species, giving a total of 144 species in our list (electronic supplementary material, table S1). We did not include cooperative birds that raise young in non-family groups in this list as all group members in these species typically attempt to breed and do not lighten the load [39]. Next, we searched for studies on each species in our list using the following search terms in Web of Science and Scopus: 'common name OR binomial species name OR synonym' (studies published up to June 2020). We also searched PhD and MSc theses, monographs published on individual species, two edited volumes on cooperatively breeding birds [37,38] and additional studies that were identified using backward and forward citation searches. Our inclusion criterion were that enough information was reported in the study to calculate any of the effect sizes described below. Our workflow is documented in electronic supplementary material, figure S1.

In total, we identified 25 studies with data on annual survival probabilities of female and male breeders. These 25 studies were on 23 different species. Female and male survival values were reported in the same study for 21 species but in separate studies from the same populations for *Malurus melanocephalus* and *Sericornis frontalis*. Annual survival was estimated using mark–recapture modelling in 5/25 studies and re-sighting probabilities in the remainder. We obtained estimates of investment in parental care (offspring feeding rates) by female and male breeders for 16/23 species for which we had survival data. For 8/16 species, these data came from the same study as the survival data (eight studies). For the eight remaining species, these data came from different studies compared with the survival data but from the same study populations (nine studies—female and male feeding rates were reported in separate studies for *Malurus cyaneus* but in the same studies for the remaining species). Finally, we obtained data on helper investment in care for 10/16 species for which we had data on breeder parental care. Helper feeding rates were reported in the same studies as breeder feeding rates for all of these species. Survival data are provided in electronic supplementary material, table S2 and feeding data in electronic supplementary material, table S3, including the figures, tables and text fragments from which data were extracted.

(b) Effect sizes

We used a statistical effect size, the natural logarithm of the rate ratio (lnRR) [40], to compare breeder survival with and without helpers (needed to address the question (a) in §1). This is breeder survival with helpers divided by breeder survival without helpers. This ratio is then log transformed to make the distribution symmetric around a value of zero—no difference in survival between breeders with and without helpers. Positive values indicate that breeder survival is higher when helped while negative values indicate that un-helped pairs have higher survival. We calculated two lnRR effect sizes for each of the 23 species in our sample, one for female breeders and one for male breeders, giving a total of 46 effect sizes.

To estimate the effect of helper presence on breeder feeding effort, we used the standardized mean difference, d (needed to address question (b) in §1). This effect size is calculated as the difference between two means, divided by their pooled sample variance [40]. In our case, d was the mean feeding effort of breeders with helpers minus the mean feeding effort of breeders without helpers. Dividing by the pooled sample variance makes the difference between means comparable across studies, which typically make measurements on different scales and have different variances. For example, feeding effort in the western bluebird was measured as the number of feeds per nestling per hour but in

the pied kingfisher this was the number of fish delivered per day to nestlings. We multiplied d by $(1 - (3/(4 \times (N_{groups} + N_{pairs} - 2) - 1)))$ to account for biases introduced by sample sizes of fewer than 10 nests (see [40]). Negative values of d indicate that breeders decrease their feeding effort when helped, positive values indicate that breeders increase their feeding effort when helped, and a value of zero indicates no difference in feeding effort between breeders in pairs and groups. Note that breeders in groups have higher fecundity than breeders in pairs in cooperative birds [39], which may increase feeding rates. However, this should make reductions in breeder care and associated increases in survival less, not more, likely. We calculated two d effect sizes for each of the 16 species for which we had data on breeder feeding effort, one for female breeders and one for male breeders, giving a total of 32 effect sizes.

Breeder survival and feeding effort were sometimes reported in groups with different numbers of helpers (e.g. groups with one helper versus groups with two helpers). When this was the case, we took weighted averages of breeder survival and feeding rates of breeders in groups to be able to calculate an effect size of the difference in survival and feeding rates between helped and un-helped breeding pairs. For example, we compared the survival of breeders in pairs with the weighted average survival of breeders with one and two helpers in the rufous treecreeper. Full details of the calculations of breeder survival and feeding effort with and without helpers, including assumptions and simplifications, are described in the electronic supplementary material, data file.

Third, we used d to estimate helper feeding effort relative to breeder feeding effort (needed to address question (c) in §1). In our case, this was: (mean feeding effort of helper − mean feeding effort of a breeder with helpers)/pooled sample variance. Again, we corrected d to account for small sample sizes. Positive values indicate that helpers feed more than breeders. In studies reporting the feeding effort of helpers in different sized groups, we calculated the total helper effort rather than the average helper effort to capture the share of total feeding performed by all helpers. We calculated two d effect sizes for each of the 10 species for which we had data on breeder feeding effort, one for female breeders and one for male breeders, giving a total of 20 effect sizes.

We calculated the inverse sampling variance of each effect size described above, which was used to weight data points in our statistical models (described below). Full details of sampling variance calculations are provided in the electronic supplementary material R script, and the sample sizes underlying these calculations are described in the electronic supplementary material, data file.

(c) Publication bias

Three different methods were used to test for publication bias (unpublished non-significant results) in each of our three effect sizes: funnel plot visualization, trim-and-fill analysis and Egger's regression [40,41]. We did not expect publication bias a priori because both significant and non-significant effects of helpers on breeder survival and feeding effort have frequently been published in the cooperative breeding literature [15,20,24–27]. Overall, there was limited evidence of publication bias in each of our effect sizes. In all three cases, the funnel plots were symmetrical (electronic supplementary material, figure S2), the intercepts from Egger's regression were all non-significantly different from zero, and the number of estimated missing studies was low for all effect sizes (effect of helper presence on breeder survival (lnRR) = 3; the effect of helper presence on breeder feeding effort (d) = 2; helper feeding effort relative to the breeder (d) = 2). Full results are reported in electronic supplementary material, table S4 along with heterogeneity (between-study variance) tests for each of our three effect sizes.

(d) Model construction

Data were analysed using Bayesian mixed-effects models in the *MCMCglmm* R package [42]. We performed three main analyses that each consisted of two parts to test if breeder survival depends on helpers moderating the costs of parental care and if this differs between the sexes. To answer our first question, (*a*), do breeders with helpers have higher annual survival than those without, we used an intercept only model with lnRR as our response variable (R code: *modApooled*). We tested for sex-specific responses of the presence of helpers on breeder survival by adding sex as a fixed effect to this model and suppressing the global intercept to estimate mean effects for females and males separately (R code: *modAsex*).

To answer our second question, (*b*), does increased breeder survival depend on reduced investment in parental care, we constructed a model with lnRR as our response variable and the effect of helper presence on breeder feeding effort (*d*) and the sample size (log transformed) associated with each estimate of *d* as fixed effects (R code: *modBpooled*). To investigate if female and male breeder survival are similarly influenced by their investment in parental care, we added sex as a third fixed effect to this model, which we interacted with *d* to estimate separate intercepts and slopes for female and male breeders (R code: *modBsex*).

To answer our third question, (*c*), does breeder investment in parental care depend on the total amount of care provided by helpers, we used a model with the effect of helper presence on breeder feeding effort (*d*) as our response variable, with helper feeding effort relative to breeder feeding effort (*d*) and the sample size (log transformed) associated with each estimate of helper feeding effort relative to breeder feeding effort included as fixed effects (R code: *modCpooled*). We tested for sex-specific responses of breeder feeding effort when helped in relation to the amount of help provided by helpers by adding sex as a third fixed effect, which we interacted with helper feeding effort relative to breeder feeding effort (*d*). This estimates separate intercepts and slopes for female and male breeders (R code: *modCsex*).

In each of the models described above, phylogenetic relationships and repeated measures from the same species (i.e. female and male values) were modelled as random effects, and each effect size was weighted by its inverse sampling variance. Phylogenetic relationships were modelled using a sample of 1300 bird trees from [43]. We ran our models on each tree in this sample sequentially for 1000 iterations per tree and saved parameter estimates from the last iteration to use as starting values for the variance components and latent variables for the next tree in the sequence. We stored 1000 iterations in total (each iteration from a different tree), after discarding the first 300 trees in the sequence as a burn-in period. Full details are given in the electronic supplementary material R script, and see [44]. We used inverse Wishart priors (variance = 1 and belief parameter = 0.002) for our random effects. We inspected traces of posterior distributions and calculated the degree of autocorrelation between successive iterations in each chain to evaluate chain mixing, and assessed model convergence using Gelman and Rubin's test [45]. We estimated the percentage of variance explained by phylogeny (I^2 phylogeny), repeated measures (I^2 repeated) and between-study effects (I^2 between) by dividing each of these variance components by the total heterogeneity [46].

Parameters reported in the Results and electronic supplementary material, table S5 are the posterior mode and 95% credible intervals (CI) of posterior distributions estimated from the *MCMCglmm* models. We also ran each of the models described above in the *metafor* R package [47] using maximum likelihood to explore the sensitivity of our results to Bayesian methods. The parameter estimates from these models were similar to those from the Bayesian models in all cases and are provided in electronic supplementary material, table S5.

Full details of model construction are given in the electronic supplementary material R script.

3. Results

(a) Does breeder survival increase with group size?

Helper presence had an overall positive effect on breeder survival across species (lnRR = 0.13, CI = 0.01 to 0.24, $N_{species} = 23$, $N_{effect\ sizes} = 46$, figure 2, electronic supplementary material, table S5). On average, breeders with helpers had an 8% higher mean rate of annual survival than breeders without helpers. There was, however, a high degree of variation between species in the effect of helpers on breeder survival. In 12/46 estimates, breeders with helpers had a significantly higher probability of surviving between years than those without. Eight of these were from female breeders and four were from male breeders. Helper presence had statistically negative effects on the survival of breeding females in green woodhoopoes and breeding males in sociable weavers.

Helpers had similar positive effects on the survival of female and male breeders across species (female lnRR = 0.11, CI = 0.01 to 0.25; male lnRR = 0.11, CI = 0.01 to 0.25, $N_{species} = 23$, $N_{effect\ sizes} = 46$, electronic supplementary material, table S5). Helpers had strongly opposing effects on breeder survival in just two species: sociable weavers and splendid fairy-wrens (figure 2). In both species, male survival decreased but female survival increased when helpers were present. Helpers had opposing but non-significant effects on breeder survival in six other species: pygmy nuthatches, acorn woodpeckers, white-browed scrub-wrens, American crows, Galapagos mockingbirds and western bluebirds (figure 2).

(b) Do increases in breeder survival depend on reduced investment in parental care?

The feeding rate of breeders with helpers was lower than the feeding rate of breeders without helpers (*d* = −0.56, CI = −0.90 to −0.26, $N_{species} = 16$, $N_{effect\ sizes} = 32$). On average, breeders contributed 25% less to feeding offspring when they had help. Reductions in breeder feeding effort in the presence of helpers had a positive effect on breeder survival, with larger reductions in feeding effort resulting in larger increases in survival (slope = −0.10, CI = −0.18 to −0.02, $N_{species} = 16$, $N_{effect\ sizes} = 32$, figure 3*a*, electronic supplementary material, table S5). Reductions in breeder feeding rates in groups versus pairs were similar for females and males (female *d* = −0.62, CI = −1.00 to −0.21; male *d* = −0.61, CI = −0.96 to −0.24, $N_{species} = 16$, $N_{effect\ sizes} = 32$) and had similar effects on breeder survival, although this was weaker for males and was not different from zero (female slope = −0.12, CI = −0.29 to −0.01; male slope = −0.07, CI = −0.20 to 0.06, electronic supplementary material, table S5; electronic supplementary material figure S3a,b).

(c) Does breeder investment in parental care depend on how much care helpers provide?

Breeders reduced their investment in feeding offspring more when they received more help (slope = −0.54, CI = −0.73 to −0.31, $N_{species} = 10$, $N_{effect\ sizes} = 20$, figure 3*b*, electronic supplementary material, table S5), consistent with the hypothesis
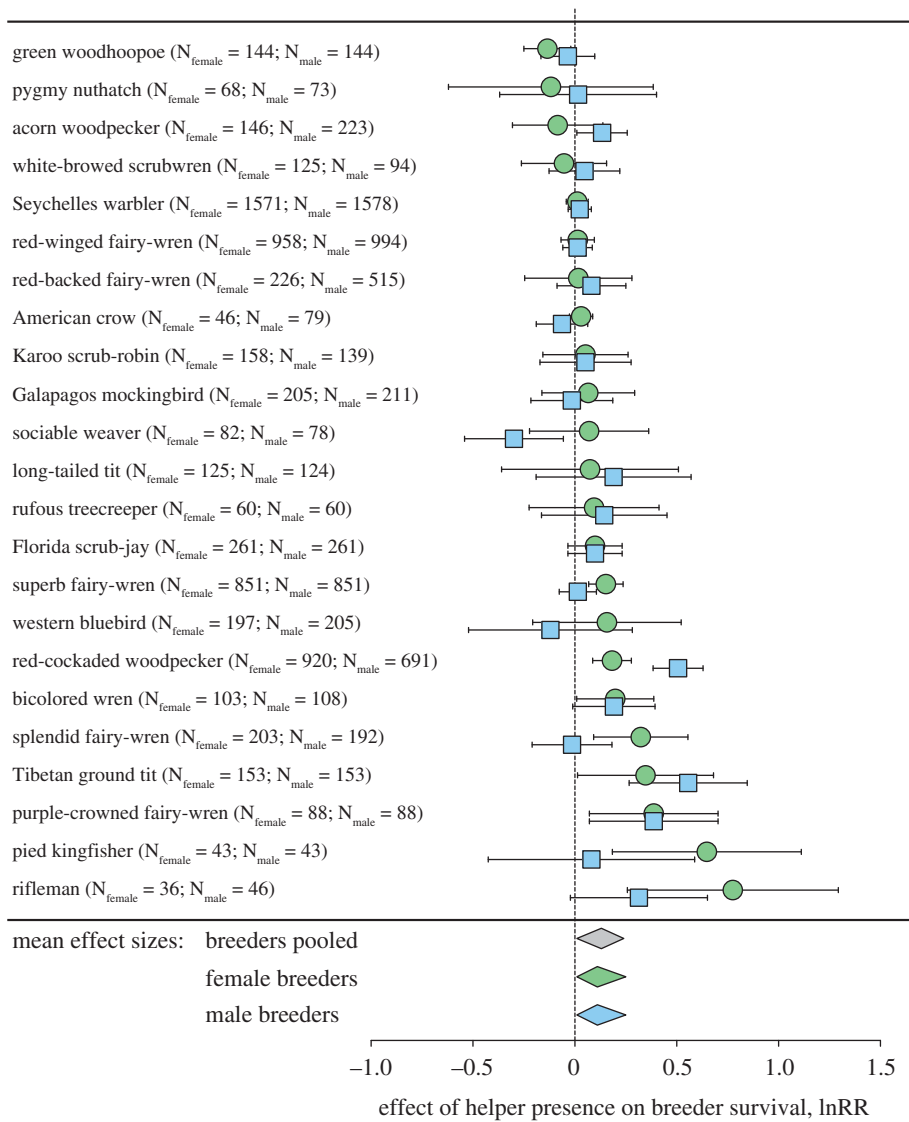
Figure 2. The difference in annual survival probability between breeders with and without helpers across 23 cooperatively breeding bird species. For each species, the natural logarithm of breeder survival with helpers divided by breeder survival without helpers (lnRR) is plotted for female (green circles) and male breeders (blue squares) separately, with 95% confidence intervals calculated from the sampling variance. Positive values of lnRR indicate that breeder survival is higher with helpers (data in electronic supplementary material, table S2).

that helpers lighten breeder workloads. This was the case for both female and male breeders when considered separately, although again the trend was weaker for males (female slope = −0.68, CI = −1.02 to −0.04; male slope = −0.47, CI = −0.93 to 0.08, electronic supplementary material, table S5; electronic supplementary material figure S3c,d).

4. Discussion

The exceptional lifespans of highly fecund breeders found in many cooperative species may, at first sight, seem inconsistent with the expectation of a trade-off between reproduction and survival [6,7]. Our results suggest that in cooperative birds, long life is partly explained by outsourcing the costs of parental care to helpers. Hard-working helpers lighten breeder workloads (figure 3b) and the energy breeders save translates into higher annual survival (figure 3a). Higher annual survival does not compromise current reproductive success as helpers are known to increase breeder fecundity in birds that breed cooperatively in family groups

[39]. The survival benefits of being helped are predicted to be more pronounced in the sex with the greater reproductive burden [19], and previous studies have highlighted that helpers lighten the load more for female breeders [20,21]. Our results, however, reveal that the survival benefits of help to male breeders are equally important (figure 2). In cooperative birds, hard-working helpers appear to be vital to alleviating the classical life-history trade-off between reproduction and survival for both sexes.

Our finding that increased breeder survival is correlated with reduced parental care (figure 3a) suggests that investment in reproduction is traded-off against longevity. However, alleviating this trade-off is just one mechanism by which helpers can increase breeder survival. Helpers could also increase breeder survival by, for example, decreasing predation risk. In many social insects, workers take on the risky tasks of foraging and defending the nest [10–12]. This protects breeders from predation, reducing breeder extrinsic mortality to such an extent that they live orders of magnitude longer than workers [10]. Helper effects on breeder survival can, therefore, occur independently of changes
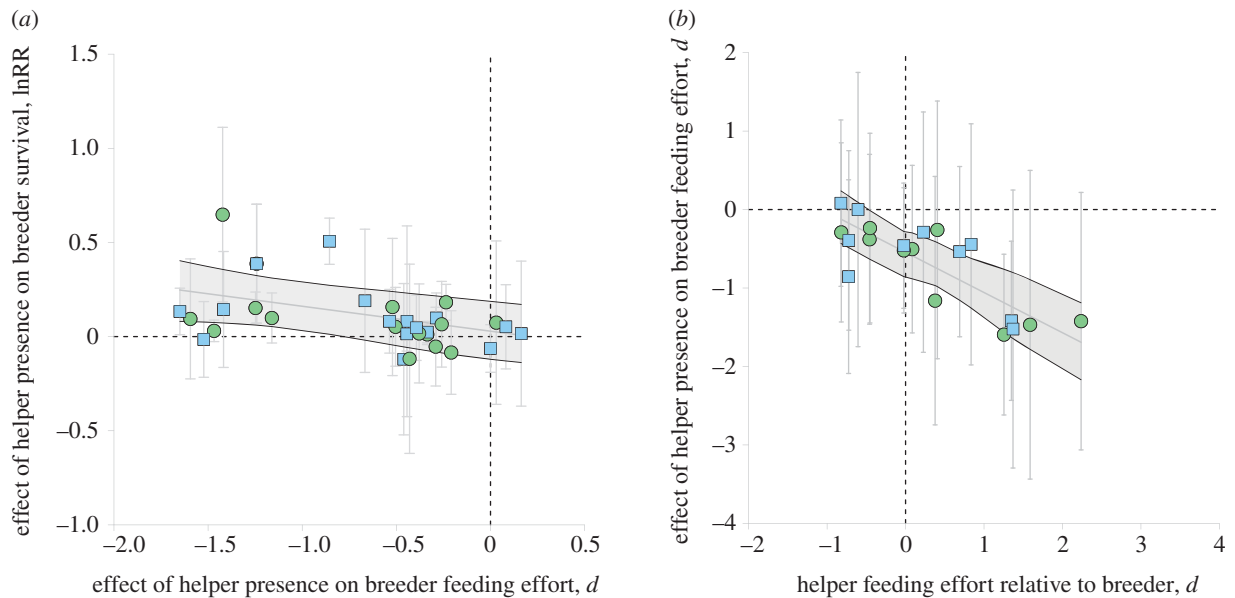
Figure 3. (a) Breeders that reduced their investment in feeding offspring to a higher degree experienced larger increases in survival ($N_{\text{species}} = 16$). (b) Breeders that received large amounts of help reduced their investment in feeding offspring more than breeders that received less help ($N_{\text{species}} = 10$). Each point is an effect size from a different species and is bracketed by its 95% confidence interval, with female (green circles) and male (blue squares) breeders shown separately. Regression lines and 95% CIs are plotted. Data are given in electronic supplementary material, table S3.

in reproductive investment, but it is clear from the data we present here that helpers influence both survival and investment in parental care.

While our results are consistent with the hypothesis that hard-working helpers extend breeder lifespans, determining causality is difficult [48,49]. In cooperative birds, high-quality breeders on good breeding territories may be more likely to recruit helpers and to live longer, creating a spurious correlation between helper presence and breeder survival. Experimental manipulations of the amount of help breeders receive, combined with the subsequent monitoring of breeder survival, are needed to infer causality. This is logistically challenging in birds but is possible in social insects, where breeders are known to be higher-quality individuals than helpers in a number of species [50,51]. Nevertheless, breeder and territory quality are not expected to cause reductions in breeder parental care that are tailored to the amount of help received. In addition, helpers are known to affect other components of breeder fitness (reproductive success) independently of the effects of breeder and territory quality in birds [52], further supporting a causal role for helpers in extending breeder lifespans.

Sex-specific survival benefits have been proposed to occur because female and male breeders can differ in how they adjust their workloads when helped, and because females carry the additional reproductive cost of laying eggs. The effect of helpers on female and male survival was generally concordant, however. One explanation for this equivalence is that the costs of parental care are extremely high in cooperative species because offspring are nidicolous (chicks remain in the nest for a long time and parental care is crucial to their survival). Both sexes, therefore, stand to make significant reductions in feeding offspring when helpers are present.

A few species in our sample did show marked differences between the sexes in how helpers affected breeder survival (figure 2). Most notably, helpers had a negative

effect on female but not male breeder survival in green woodhoopoes and a negative effect on male but not female breeder survival in sociable weavers. A number of factors have been linked to sex differences in lifespan in non-cooperative species, for example, variation in the trade-off between current reproduction and survival and the relative strengths of sexual selection in females and males [53,54]. These are likely to be important factors shaping sex-specific responses of breeders to helpers in cooperative species. For example, reproductive competition in green woodhoopoes increases the physiological costs of reproduction and reduces survival in females, but not males [55]. In sociable weavers, reduced survival of breeding males could result from the reproductive competition with helpers to mate with the breeding female, to whom nearly a third of male helpers are unrelated [21].

In summary, our results show that hard-working helpers can contribute to the evolution of extended breeder lifespans. While the trade-off between reproduction and survival is relatively well investigated in non-cooperative species, how outsourcing parental care to helpers shapes life-history evolution in cooperative species requires greater empirical and theoretical attention. For example, why are load-lightening effects prominent in some species but not others, why does reduced investment in parental care by breeders translate into higher survival in some species but higher fecundity in others, and to what extent is load-lightening dependent upon environmental conditions? By characterizing the generality of helper effects on breeder survival we hope this study stimulates further research into the underlying mechanisms shaping the extraordinary life-histories of cooperative species.

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References

1. Peterson C, Nagy K, Diamond J. 1990 Sustained metabolic scope. *Proc. Natl Acad. Sci. USA* **87**, 2324–2328. (doi:10.1073/pnas.87.6.2324)

2. Dijkstra C, Bult A, Bijlsma S, Daan S, Meijer T, Zijlstra, M. 1990 Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and parent survival. *J. Anim. Ecol.* **59**, 269–285. (doi:10.2307/5172)

3. Magnhagen C. 1991 Predation risk as a cost of reproduction. *Trends Ecol. Evol.* **6**, 183–186. (doi:10.1016/0169-5347(91)90210-0)

4. Koivula M, Koskela E, Mappes T, Oksanen TA. 2003 Cost of reproduction in the wild: manipulation of reproductive effort in the bank vole. *Ecology* **84**, 398–405. (doi:10.1890/0012-9658(2003)084[0398:CORITW]2.0.CO;2)

5. Royle NJ, Smiseth PT, Kölliker M. 2012 *The evolution of parental care*. Oxford, UK: Oxford University Press.

6. Williams GC. 1966 Natural selection, the costs of reproduction and a refinement of Lack's principle. *Am. Nat.* **100**, 687–690. (doi:10.1086/282461)

7. Stearns SC. 1992 *The evolution of life histories*. Oxford, UK: Oxford University Press.

8. Hamel S, Gaillard JM, Yoccoz NG, Loison A, Bonenfant C, Descamps S. 2010 Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. *Ecol. Lett.* **13**, 915–935. (doi:10.1111/j.1461-0248.2010.01478.x)

9. Santos ES, Nakagawa S. 2012 The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. *J. Evol. Biol.* **25**, 1911–1917. (doi:10.1111/j.1420-9101.2012.02569.x)

10. Keller L, Genoud M. 1997 Extraordinary lifespans in ants: a test of evolutionary theories of ageing. *Nature* **389**, 958–960. (doi:10.1038/40130)

11. Downing PA, Cornwallis CK, Griffin AS. 2017 How to make a sterile helper. *Bioessays* **39**, 1600136. (doi:10.1002/bies.201600136)

12. Hölldobler B, Wilson EO. 1990 *The ants*. Boston, MA: Harvard University Press.

13. Dammann P *et al.* 2011 Extended longevity of reproductives appears to be common in *Fukomys* mole-rats (Rodentia, Bathyergidae). *PLoS ONE* **6**, e18757. (doi:10.1371/journal.pone.0018757)

14. Austad SN, Rabenold KN. 1985 Reproductive enhancement by helpers and an experimental inquiry into its mechanism in the bicolored wren. *Behav. Ecol. Soc.* **17**, 19–27. (doi:10.1007/BF00299423)

15. Austad SN, Rabenold KN. 1986 Demography and the evolution of cooperative breeding in the bicolored wren, *Campylorhynchus griseus*. *Behaviour* **97**, 308–324. (doi:10.1163/156853986X00667)

16. Brown JL. 1978 Avian communal breeding systems. *Annu. Rev. Ecol. Sys.* **9**, 123–155. (doi:10.1146/annurev.es.09.110178.001011)

17. Crick HQ. 1992 Load-lightening in cooperatively breeding birds and the cost of reproduction. *Ibis* **134**, 56–61. (doi:10.1111/j.1474-919X.1992.tb07230.x)

18. Heinsohn RG. 2004 Parental care, load-lightening and costs. In *Ecology and evolution of cooperative breeding in birds* (eds W Koenig, J Dickinson), pp. 67–80. Cambridge, UK: Cambridge University Press.

19. Johnstone RA. 2011 Load lightening and negotiation over offspring care in cooperative breeders. *Behav. Ecol.* **22**, 436–444. (doi:10.1093/beheco/arq190)

20. Rood JP. 1990 Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Anim. Behav.* **39**, 566–572. (doi:10.1016/S0003-3472(05)80423-3)

21. Paquet M, Doutrelant C, Hatchwell BJ, Spottiswoode CN, Covas R. 2015 Antagonistic effect of helpers on breeding male and female survival in a cooperatively breeding bird. *J. Anim. Ecol.* **84**, 1354–1362. (doi:10.1111/1365-2656.12377)

22. Sydeman WJ. 1989 Effects of helpers on nestling care and breeder survival in pygmy nuthatches. *Condor* **91**, 147–155. (doi:10.2307/1368158)

23. Shreeves G, Field J. 2002 Group size and direct fitness in social queues. *Am. Nat.* **159**, 81–95. (doi:10.1086/324125)

24. Khan M, Walters J. 2002 Effects of helpers on breeder survival in the red-cockaded woodpecker (*Picoides borealis*). *Behav. Ecol. Sociobiol.* **51**, 336–344. (doi:10.1007/s00265-001-0441-3)

25. Lloyd P, Martin TE, Taylor A, Braae A, Altwegg R. 2016 Age, sex and social influences on adult survival in the cooperatively breeding Karoo scrub-robin. *Emu* **116**, 394–401. (doi:10.1071/MU15076)

26. Creel S, Creel NM. 2015 Opposing effects of group size on reproduction and survival in African wild dogs. *Behav. Ecol.* **26**, 1414–1422. (doi:10.1093/beheco/arv100)

27. du Plessis MA. 1993 Helping behavior in cooperatively breeding green woodhoopoes: selected or unselected trait. *Behaviour* **127**, 49–65. (doi:10.1163/156853993X00425)

28. Cant MA, Field J. 2001 Helping effort and future fitness in cooperative animal societies. *Proc. R. Soc. Lond. B* **268**, 1959–1964. (doi:10.1098/rspb.2001.1754)

29. Green JP, Freckleton RF, Hatchwell BJ. 2016 Variation in helper effort among cooperatively breeding bird species is consistent with Hamilton's Rule. *Nat. Commun.* **7**, 12663. (doi:10.1038/ncomms12663)

30. Kingma SA. 2017 Direct benefits explain interspecific variation in helping behaviour among cooperatively breeding birds. *Nat. Commun.* **8**, 1094. (doi:10.1038/s41467-017-01299-5)

31. Downing PA, Griffin AS, Cornwallis CKC. 2018 Sex differences in helping effort reveal the effect of future reproduction on cooperative behaviour in birds. *Proc. R. Soc. B* **285**, 20181164. (doi:10.1098/rspb.2018.1164)

32. Guindre-Parker S, Rubenstein DR. 2020 Survival benefits of group living in a fluctuating environment. *Am. Nat.* **195**, 1027–1036. (doi:10.1086/708496)

33. Kingma SA, Hall ML, Arriero E, Peters A. 2010 Multiple benefits of cooperative breeding in purple-crowned fairy-wrens: a consequence of fidelity? *J. Anim. Ecol.* **79**, 757–768. (doi:10.1111/j.1365-2656.2010.01697.x)

34. Hammers M *et al.* 2019 Breeders that receive help age more slowly in a cooperatively breeding bird. *Nat. Commun.* **10**, 1301. (doi:10.1038/s41467-019-09229-3)

35. Luck GW. 2001 The demography and cooperative breeding behaviour of the rufous treecreeper. *Climacteris rufa. Aus. J. Zoo.* **49**, 515–537. (doi:10.1071/ZO00087)

36. Lloyd P, Taylor WA, du Plessis MA, Martin TE. 2009 Females increase reproductive investment in response to helper-mediated improvements in allo-feeding, nest survival, nestling provisioning and post-fledging survival in the Karoo scrub-robin *Cercotrichas coryphaeus*. *J. Avian Biol.* **40**, 400–411. (doi:10.1111/j.1600-048X.2008.04642.x)

37. Stacey PB, Koenig WD (eds). 1990 *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge, UK: Cambridge University Press.

38. Koenig WD, Dickinson JL (eds). 2016 *Cooperative breeding in vertebrates: studies of ecology, evolution and behavior*. Cambridge, UK: Cambridge University Press.

39. Downing PA, Griffin AS, Cornwallis CKC. 2020 Group formation and the evolutionary pathway to complex sociality in birds. *Nat. Ecol. Evol.* **4**, 479–486. (doi:10.1038/s41559-020-1113-x)

40. Koricheva J, Gurevitch J, Mengersen K (eds). 2013 *Handbook of meta-analysis in ecology and evolution*. Princeton, NJ: Princeton University Press.

41. Nakagawa S, Noble DWA, Senior AM, Lagisz M. 2017 Meta-evaluation of meta-analysis: ten

appraisal questions for biologists. *BMC Biol.* **15**, 18. (doi:10.1186/s12915-017-0357-7)

42. Hadfield JD. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Soft.* **33**, 1–22. (doi:10.18637/jss.v033.i02)

43. Jet, W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012 The global diversity of birds in space and time. *Nature* **491**, 444–448. (doi:10.1038/nature11631)

44. Ross L, Gardner A, Hardy N, West SA. 2013 Ecology, not the genetics of sex determination, determines who helps in eusocial populations. *Curr. Biol.* **23**, 2383–2387. (doi:10.1016/j.cub.2013.10.013)

45. Gelman A, Rubin DB. 1992 Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**, 457–511. (doi:10.1214/ss/1177011136)

46. Nakagawa S, Santos ESA. 2012 Methodological issues and advances in biological meta-analysis.

Evol. Ecol. **26**, 1253–1274. (doi:10.1007/s10682-012-9555-5)

47. Viechtbauer W. 2010 Conducting meta-analyses in R with the metafor package. *J. Stat. Soft.* **36**, 1–48. (doi:10.18637/jss.v036.i03)

48. Rowley I. 1965 The life history of the superb blue wren, *Malurus cyaneus*. *Emu* **64**, 251–297. (doi:10.1071/MU964251)

49. Brown JL, Brown ER, Brown SD, Dow DD. 1982 Helpers: effects of experimental removal on reproductive success. *Science* **215**, 421–422. (doi:10.1126/science.215.4531.421)

50. Blacher P, Huggins TJ, Bourke AFG. 2017 Evolution of ageing, costs of reproduction and the fecundity–longevity trade-off in eusocial insects. *Proc. R. Soc. B* **284**, 20170380. (doi:10.1098/rspb.2017.0380)

51. Shell WA, Rehan SM. 2018 The price of insurance: costs and benefits of worker production in a

facultatively social bee. *Behav. Ecol.* **29**, 204–211. (doi:10.1093/beheco/arx146)

52. Downing PA, Griffin AS, Cornwallis CK. 2020 The benefits of help in cooperative birds: nonexistent or difficult to detect? *Am. Nat.* **195**, 1085–1091. (doi:10.1086/708515)

53. Bonduriansky R, Maklakov A, Zajitschek F, Brooks R. 2008 Sexual selection, sexual conflict and the evolution of ageing and life span. *Funct. Ecol.* **22**, 443–453. (doi:10.1111/j.1365-2435.2008.01417.x)

54. Maklakov AA, Lummaa V. 2013 Evolution of sex differences in lifespan and aging: causes and constraints. *Bioessays* **35**, 717–724. (doi:10.1002/bies.201300021)

55. Hawn AT, Radford AN, du Plessis MA. 2007 Delayed breeding affects lifetime reproductive success differently in male and female green woodhoopoes. *Curr. Biol.* **17**, 844–849. (doi:10.1016/j.cub.2007.03.036)

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