

Hard-working Helpers Contribute to Long Breeder Lifespans in Cooperative Birds

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- READ ME
- R script
- Data for effect size calculations
- Table S1: species searched
- Table S2: survival data
- Table S3: data on offspring feeding effort
- Table S4: publication bias tests
- Table S5: model results
- Data in long format to read into R
- Figures S1, S2 and S3: PRISMA flow chart, funnel plots and sex-specific effects

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Abstract

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. Female and male breeders showed similar patterns. Our results indicate that one of the secrets to long life is reduced investment in parental care. This appears to be a unique feature of cooperative societies with hard-working helpers.

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 and 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 to 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

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 (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 criteria were that enough information was reported in the study to calculate any of the effect sizes described below. Our workflow is documented in 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 modeling 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, this data came from the same study as the survival data (eight studies). For the eight remaining species this data came from different studies to 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 table S2 and feeding data in table S3, including the figures, tables and text fragments from which data were extracted.

Effect sizes

We used a statistical effect size, the natural logarithm of the rate ratio ($\ln RR$) [40], to compare breeder survival with and without helpers (needed to address question *a*). This is simply breeder survival with helpers divided by breeder survival without helpers. This ratio is then log transformed to make the distribution symmetric with a null 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 $\ln RR$ 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*). This effect size is calculated as the

151 difference between two means, divided by their pooled sample variance [40]. In our case d
 152 was the mean feeding effort of breeders with helpers minus the mean feeding effort of
 153 breeders without helpers. Dividing by the pooled sample variance makes the difference
 154 between means comparable across studies, which typically make measurements on different
 155 scales and have different variances. For example, feeding effort in the western bluebird was
 156 measured as the number of feeds / nestling / hour but in the pied kingfisher this was the
 157 number of fish delivered / day to nestlings. We multiplied d by $(1 - (3 / (4 * (N_{groups} + N_{pairs} -$
 158 $2) - 1)))$ to account for biases introduced by sample sizes of less than 10 nests (see [40]).
 159 Negative values of d indicate that breeders decrease their feeding effort when helped, positive
 160 values indicate that breeders increase their feeding effort when helped and a value of zero
 161 indicates no difference in feeding effort between breeders in pairs and groups. Note that
 162 breeders in groups have higher fecundity than breeders in pairs in cooperative birds [39],
 163 which may increase feeding rates. However, this should make reductions in breeder care and
 164 associated increases in survival less, not more, likely. We calculated two d effect sizes for
 165 each of the 16 species for which we had data on breeder feeding effort, one for female
 166 breeders and one for male breeders, giving a total of 32 effect sizes.
 167
 168 Breeder survival and feeding effort were sometimes reported in groups with different numbers
 169 of helpers (e.g. groups with one helper vs. groups with two helpers). When this was the case,
 170 we took weighted averages of breeder survival and feeding rates of breeders in groups to be
 171 able to calculate an effect size of the difference in survival and feeding rates between helped
 172 and un-helped breeding pairs. For example, we compared the survival of breeders in pairs
 173 with the weighted average survival of breeders with one and two helpers in the rufous
 174 treecreeper. Full details of the calculations of breeder survival and feeding effort with and

without helpers, including assumptions and simplifications, are described in the supplementary data file.

Third, we used d to estimate helper feeding effort relative to breeder feeding effort (needed to address question *c*). In our case this was: (mean feeding effort of helper – mean feeding effort of 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 were used to weight data points in our statistical models (described below). Full details of sampling variance calculations are provided in the supplementary R script and the sample sizes underlying these calculations are described in the supplementary data file.

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 (figure S2), the intercepts from Egger's regression were all non-significantly different from zero, and the number of estimated missing studies were low for all effect sizes (effect of helper presence on breeder survival ($\ln RR$) = 3; the effect of helper presence on breeder feeding effort (d) = 2; helper feeding effort relative to breeder (d) = 2). Full results are reported in table S4 along with heterogeneity (between-study variance) tests for each of our three effect sizes.

Model construction

Data were analyzed 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 $\ln RR$ 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 $\ln RR$ 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 supplementary 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 used 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 section and 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 table S5. Full details of model construction are given in the supplementary R script.

3. Results

a) Does breeder survival increase with group size?

Helper presence had an overall positive effect on breeder survival across species ($\ln RR = 0.13$, CI = 0.01 to 0.24, $N_{species} = 23$, $N_{effect\ sizes} = 46$, figure 2, 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 $\ln RR = 0.11$, CI = 0.01 to 0.25; male $\ln RR = 0.11$, CI = 0.01 to 0.25, $N_{species} = 23$, $N_{effect\ sizes} = 46$, 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 3a, 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 , table S5; 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 3b, table S5), consistent with the hypothesis 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, 95% CI = -0.93 to 0.08, table S5; 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 – 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 and has reduced 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 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 [52], further supporting a causal role for helpers in extending breeder lifespans.

We expected to find sex-specific survival benefits because of differences between female and male breeders 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 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. This provides an additional survival benefit to that which arises from the reduced the risk of predation in larger groups [10,11]. 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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Figures



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 used the following images from the Macaulay Library at the Cornell Lab of Ornithology: ML76482571, ML193642671, ML257993281, ML252195471.

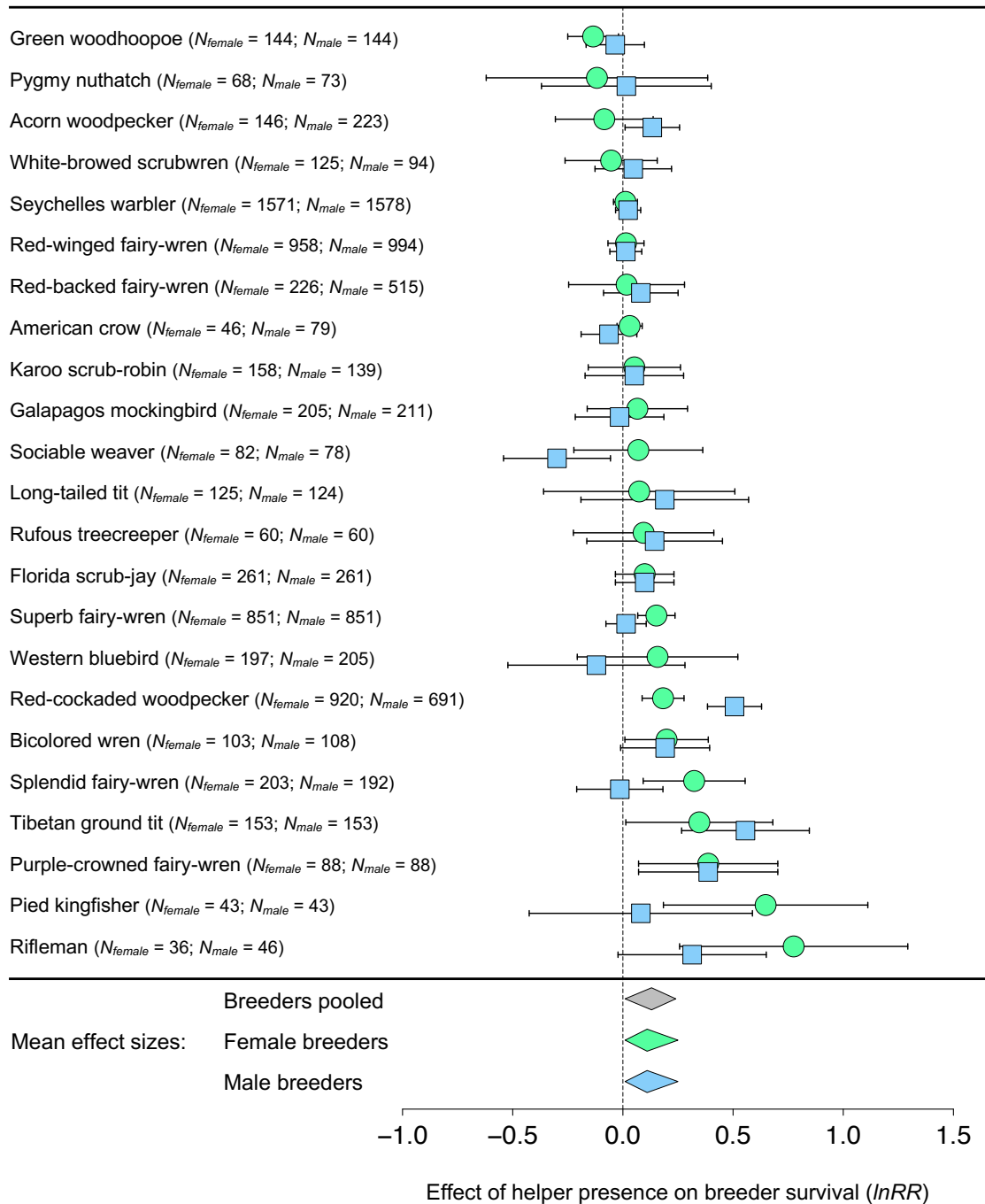
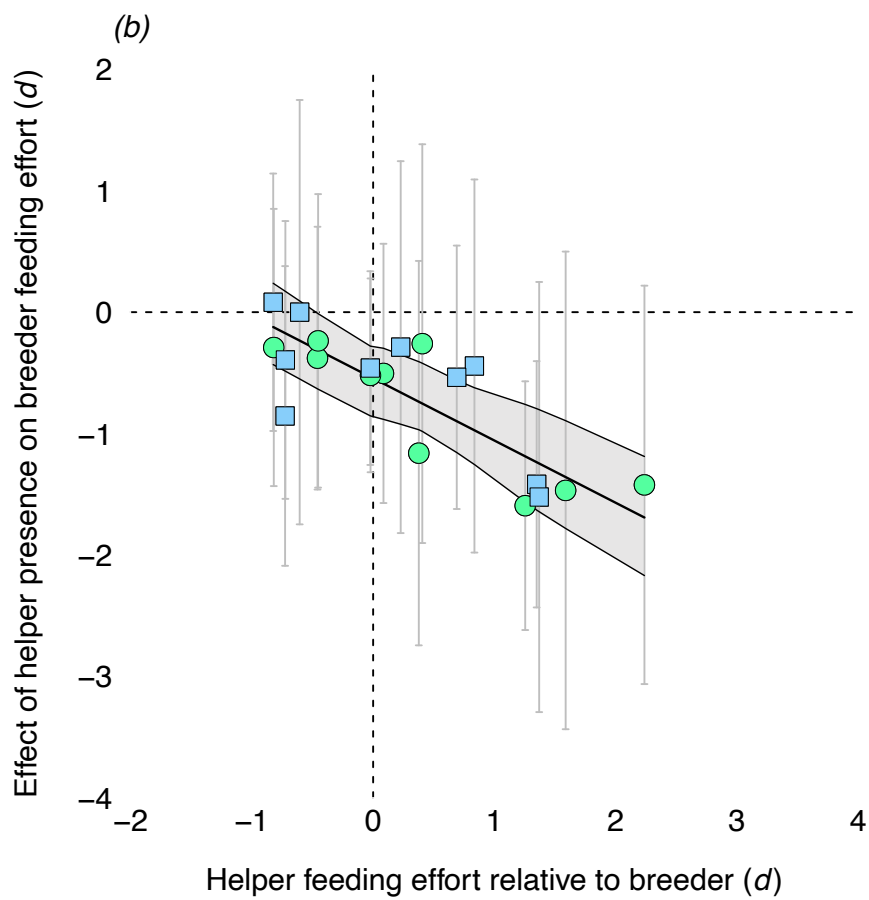
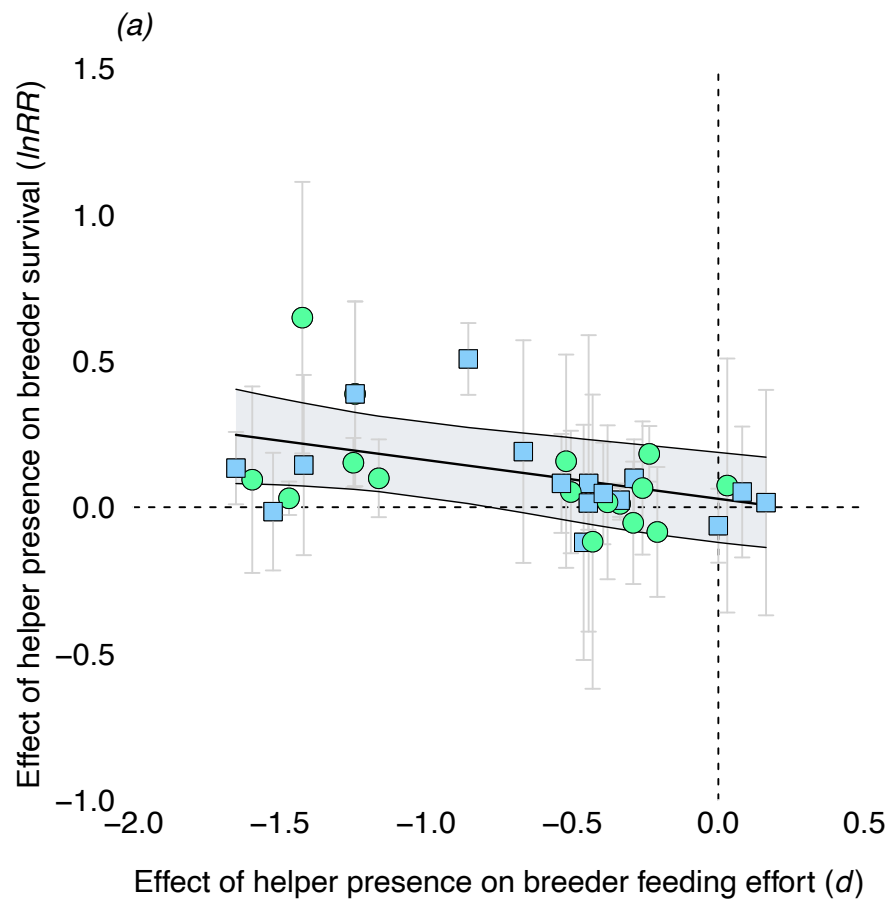


Figure 2. The difference in annual survival probability between breeders with and without helpers across 23 cooperatively breeding bird species. For each species, the natural logarithm of breeder survival with helpers divided by breeder survival without helpers ($\ln RR$) is plotted for female (green circles) and male breeders (blue squares) separately, with 95% confidence intervals calculated from the sampling variance. Positive values of $\ln RR$ indicate that breeder survival is higher with helpers (data in table S2).



537 Figure 3. (a) Breeders that reduced their investment in feeding offspring to a higher degree
538 experienced larger increases in survival ($N_{species} = 16$). (b) Breeders that received large
539 amounts of help reduced their investment in feeding offspring more than breeders that
540 received less help ($N_{species} = 10$). Each point is an effect size from a different species and is
541 bracketed by its 95% confidence interval, with female (green circles) and male (blue squares)
542 breeders shown separately. Regression lines and 95% CIs are plotted. Data in table S3.