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Cite this article: Downing PA, Cornwallis CK, Griffin AS. 2015 Sex, long life and the evolutionary transition to cooperative breeding in birds. *Proc. R. Soc. B* **282**: 20151663. <http://dx.doi.org/10.1098/rspb.2015.1663>

Received: 10 July 2015

Accepted: 1 September 2015

Subject Areas:

behaviour, evolution

Keywords:

inclusive fitness, birds, promiscuity, survival, life-history evolution

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2015.1663> or via <http://rspb.royalsocietypublishing.org>.

Sex, long life and the evolutionary transition to cooperative breeding in birds

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Long life is a typical feature of individuals living in cooperative societies. One explanation is that group living lowers mortality, which selects for longer life. Alternatively, long life may make the evolution of cooperation more likely by ensuring a long breeding tenure, making helping behaviour and queuing for breeding positions worthwhile. The benefit of queuing will, however, depend on whether individuals gain indirect fitness benefits while helping, which is determined by female promiscuity. Where promiscuity is high and therefore the indirect fitness benefits of helping are low, cooperation can still be favoured by an even longer life span. We present the results of comparative analyses designed to test the likelihood of a causal relationship between longevity and cooperative breeding by reconstructing ancestral states of cooperative breeding across birds, and by examining the effect of female promiscuity on the relationship between these two traits. We found that long life makes the evolution of cooperation more likely and that promiscuous cooperative species are exceptionally long lived. These results make sense of promiscuity in cooperative breeders and clarify the importance of life-history traits in the evolution of cooperative breeding, illustrating that cooperation can evolve via the combination of indirect and direct fitness benefits.

1. Introduction

Individuals help raise young produced by others in approximately one-tenth of all bird species [1,2]. Such cooperative breeding systems are often characterized by the delayed dispersal of young leading to social queuing for territorial inheritance and the acquisition of a breeding position [3,4]. For example, while many passerines breed in their first year of adulthood [5], superb fairy-wrens, *Malurus cyaneus*, normally delay reproduction for two breeding seasons, during which time they help to raise the young in their group before becoming dominant breeders [6]. Social queues of this kind reach their extreme in white-winged choughs, *Corcorax melanorhamphos*, in which individuals delay breeding until they are at least 4 years of age, during which time they help to build the nest, incubate and feed the young, and participate in group defence [7].

Observations of this kind led to the prediction that long life drives the evolution of cooperative breeding: only in long-lived species will individuals survive to breed after queuing [8,9]. Pen & Weissing's [10] theoretical model of the evolution of cooperative breeding supports this. They found that long life increases the probability that cooperation will evolve because it lengthens an individual's breeding tenure, enhancing its direct fitness. In contrast with verbal models [11,12], this relationship results regardless of any ecological constraints on reproduction such as slow territory turnover. Theoretical evidence to date therefore suggests that long life increases the likelihood of cooperation evolving. Consistent with this prediction, comparative analyses have demonstrated that cooperative breeders are longer lived than non-cooperative breeders [11,13,14]. This finding, however, is also consistent with the alternative prediction that long life evolves as a result of cooperative breeding: group living protects individuals from extrinsic causes of mortality, which thus selects for longer life [15,16]. It is therefore unclear to what extent the association between long life and cooperative breeding is due to long-lived species being

predisposed towards cooperation or is simply a response to the protective benefits offered by group living.

Although long life has been predicted to be important in the evolution of cooperation by increasing future direct fitness benefits [10,17], the influence of indirect fitness benefits in relation to longevity remains to be explored. The potential for helpers to gain indirect fitness is determined by relatedness to the offspring they care for. In a family group, relatedness among offspring is typically determined by whether female breeders mate with multiple males [18,19]. Under strict monogamy, helpers are as related to their nest-mates, which are full siblings, as they are to their own offspring ($r = 0.5$ in both cases), reducing the fitness differential between reproduction and helping. Indeed, monogamy makes the evolution of cooperative breeding more likely in both birds [20] and mammals [21] (see also Hughes *et al.*'s [22] analysis of the effect of monogamy on transitions to eusociality in the social insects). When breeding females of cooperative species are promiscuous, the loss of indirect fitness benefits may be compensated for by an extended life span that increases reproductive success in the future. We can therefore make the testable prediction that promiscuous cooperative species will be relatively longer lived than monogamous cooperative species.

Here we use phylogenetic analyses across birds to verify key assumptions of current research, and to expand our understanding of how the interaction between direct and indirect fitness benefits influences the origin of cooperative breeding and its relationship with longevity. More specifically, we show (i) that helpers queue for reproductive positions and during this time they have limited access to direct reproduction, (ii) that cooperative breeders are indeed longer lived than non-cooperative breeders, (iii) that long life preceded the evolution of cooperative breeding rather than evolving as a result of group living and (iv) that life span is longer in cooperative breeders that have high levels of female promiscuity, whereas monogamous cooperative breeders have similar longevity to non-cooperative breeders.

2. Material and methods

(a) Data collection

In Pen & Weissing's model [10], individuals have the choice to stay at the natal nest and become a helper, or to disperse and find a new nest elsewhere. To test the predictions resulting from their model, we therefore defined cooperative breeding as a breeding system in which at least 10% of young are retained on their natal territory and provide care to siblings. Consequently, polyandrous species (such as the dunnock and Galapagos hawk) or plural breeding systems without natal philopatry (such as that of the greater ani, where direct fitness benefits are thought to play a key role in maintaining cooperative behaviour [23–25]) are excluded from our definition of cooperation.

We obtained data on whether cooperative breeders queue for breeding positions via keyword searches including the terms 'species name AND demography OR reproduction' using Web of Science and Google Scholar up to and including 10 March 2015, as well as forward and backward citation searches based on these studies. We considered only the philopatric sex given that the predictions of the quantitative models we are testing relate to this sex. We obtained data on the ages at which individuals first bred for 39 species of bird (cooperative $n_{\text{species}} = 19$, non-cooperative $n_{\text{species}} = 20$; electronic supplementary material,

table S1). This is the most complete sample we could obtain for cooperative breeders, while the sample of non-cooperative breeders were chosen to give a balanced design and are randomly distributed across avian families, encompassing approximately the same degree of phylogenetic diversity as cooperative species.

To investigate whether life span is a cause or a consequence of cooperation we collected data on all species of bird for which published information on extra-pair paternity and survival parameters were available. We started with the species included in an analysis of promiscuity rates and cooperative breeding in birds published by Cornwallis *et al.* [20], and updated this list to include recently published data on extra-pair paternity up to and including 10 March 2015. We collected data on three potential measures of life span: annual survival, average survival and maximum longevity. These were found through keyword searches using the terms 'species name AND survival OR longevity' using Web of Science and Google Scholar up to and including 10 March 2015. We also carried out forward and backward citation searches on major reviews [14,26–29]. Our different measures of survival were highly correlated (electronic supplementary material, figure S1*a–c*). We used annual survival in our analyses as these estimates are typically based on wild populations with the largest sample sizes, and as such are less susceptible to outliers than estimates of maximum and average survival [14]. In total, we compiled survival and promiscuity estimates for 238 species of bird (cooperative $n_{\text{species}} = 35$, non-cooperative $n_{\text{species}} = 203$; electronic supplementary material, table S2).

We measured female promiscuity as the percentage of broods with at least one extra-group chick. When testing for a difference in survival between cooperative and non-cooperative breeders, we controlled for a number of covariates that are known to influence survival: promiscuity [30], body mass [27,31–33] and latitude [27,34]. We collected data on body mass (grams) from the *Handbook of the birds of the world* [35] and on latitude from the studies reporting survival for each species in our dataset.

To account for non-independence between species owing to shared evolutionary history [36] we adopted a comparative approach analysing data using Bayesian phylogenetic linear mixed models (BPMs) [37–39]. BPMs take a phylogenetic tree and convert it into a variance–covariance matrix that represents all pairwise 'evolutionary' distances between species that enables the variance in response traits that arises due to phylogenetic history to be estimated. These methods are well suited to the type of data we have collected, where species have not been systematically studied with respect to their position in the phylogeny. To account for phylogenetic uncertainty, we repeated each of our analysis on 10 bird trees ($n_{\text{species}} = 9993$), each a maximum clade credibility (MCC) consensus tree constructed from 1000 posterior samples from a recent bird phylogeny generated under a Bayesian inference framework [40]. Each tree was trimmed to match the number of species in each analysis. Posterior samples from each of the 10 models were combined for parameter estimation.

(b) Analyses

We performed four sets of analyses using BPMs conducted in MCMCglmm [41] in R v. 3.0.2 [42]. First, we asked whether cooperative breeders queue for breeding positions by testing if the mean age at first reproduction differs between cooperative and non-cooperative species. We modelled mean age at first reproduction as our response variable (modelled using a Gaussian distribution) with breeding system (two-level factor: cooperative versus non-cooperative) and mass (covariate) included as fixed effects. Mass and mean age at first reproduction were log and Z-transformed (mean of 0 and standard deviation of 1). We then tested if the proportion of individuals breeding in different

age classes differs between cooperative and non-cooperative species. Our response was the proportion of individuals breeding at each age (modelled using a binomial distribution with a logit link function), with mass (covariate), breeding system (two-level factor: cooperative versus non-cooperative), age (covariate) and the interaction between breeding system and age as fixed effects. We specified species identity and its interaction with age as random effects to account for repeated measures on the same species across different ages. An unstructured covariance matrix was specified for the interaction between species and age allowing intercepts and slopes to vary to account for the possibility that species may differ in the proportion of individuals breeding over age [43]. We then investigated whether helpers gain a significant amount of direct fitness while queuing. Using the data collected on extra-pair paternity, we determined the number of young sired by dominant breeders and the number of young sired by helpers for as many cooperative species as possible ($n_{\text{species}} = 40$; note that five species in this analysis did not have survival data). If reproduction within groups is shared in an egalitarian way, we would expect half of the young to be sired by dominant individuals and half to be sired by subordinate individuals. To determine the proportion of young sired by dominant individuals, we modelled the number of offspring sired by dominants and subordinates as the response variable (using a binomial distribution with a logit link function) with the intercept fitted as a fixed effect and a phylogenetic covariance matrix fitted as a random effect. We calculated the posterior mode and 95% credible interval (CI) for the intercept to estimate the relative reproductive success of dominant and subordinate individuals, and tested if this differed from 50:50 by examining if the CI encompassed 50%.

Second, to confirm that cooperative breeders are longer lived than non-cooperative breeders, we modelled annual survival as the response variable (using a binomial distribution with a logit link function) with mass (covariate), latitude (covariate), promiscuity (covariate) and breeding system (two-level factor: cooperative versus non-cooperative) fitted as fixed effects. Prior to analyses, we arcsine-square-root-transformed promiscuity as it is percentage data, mass was log-transformed and both were Z-transformed (mean of 0 and standard deviation of 1).

Third, we examined whether evolutionary transitions to and from cooperative breeding were predicted by increases and decreases in survival, respectively. We adopted three complementary approaches. First, we tested whether survival and cooperation are correlated through evolutionary time by constructing a multi-response BPMM. We fitted survival as a binomial response and the probability of being cooperative (0 is non-cooperative, 1 is cooperative) as a binary response. We removed the global intercept from the model, fitting separate intercepts for each trait. To estimate the phylogenetic correlation between traits we fitted a 2×2 variance-covariance matrix for the interaction between trait and phylogeny and calculated the correlation as $\text{COV}_{\text{survival/cooperative}}/\sqrt{\text{VAR}_{\text{survival}} \times \text{VAR}_{\text{cooperative}}}$. We also fitted a 2×2 residual variance-covariance matrix to allow for different error variances and covariance across the two traits. A significant positive phylogenetic correlation between survival and cooperation would indicate that the evolution of cooperative breeding is associated with increases in survival through evolutionary time. This approach, however, does not reveal the ordering of evolutionary events. We therefore compared levels of survival between the ancestors of non-cooperative and cooperative species to determine whether long-lived non-cooperative species were more likely to have cooperative descendants than short-lived non-cooperative species. This was done by using BPMMs (binary response variable: 0 is non-cooperative, 1 is cooperative) to reconstruct ancestral states of cooperative breeding. We classified nodes as being cooperative if the posterior probability was greater than 0.95, and non-cooperative if it was less than

0.05. Using reconstructed states we classified each node on each of the 10 phylogenies according to its predicted breeding system and the breeding systems of its descendants. Four transitions were possible: (i) a gain of cooperation (a non-cooperative ancestor with a cooperative descendant), (ii) a loss of cooperation (a cooperative ancestor with a non-cooperative descendant), (iii) no change (a cooperative ancestor with a cooperative descendant) and (iv) no change (a non-cooperative ancestor with a non-cooperative descendant). These nodal classifications were then fitted as the explanatory variable (four-level fixed factor) in a BPMM with survival as the response (using a binomial distribution with a logit link function) and a phylogenetic covariance matrix linked to ancestral nodes included as a random effect. This model estimates survival at each of the internal nodes in the phylogeny and tests whether there are differences in survival among the four transition categories. We accounted for uncertainty in our ancestral state reconstructions by repeating the analysis 100 times, every time reclassifying nodes by resampling from the posterior distribution of the probability of each node being cooperative or non-cooperative from the original model used to reconstruct ancestral states of cooperative breeding. We then combined posterior samples from across the 100 models. Finally, we used the BAYES TRAITS [44] DISCRETE module with MCMC sampling to test whether the evolution of cooperation is more likely given a long life span than a short life span. As BAYES TRAITS requires binary characters, we assigned species equal to or greater than the median level of survival as long lived and those less than the median as short lived. Transition rates were assessed by constructing a model where we restricted gains of cooperation to be the same regardless of life span and a model where we restricted gains of long life to be the same regardless of cooperation. We combined the posterior distribution of five independent runs from each model to ensure that transition rate estimates were stable and accurate, and accounted for phylogenetic uncertainty by including the same 10 MCC trees used in the above analyses. We compared model support using Bayes factors.

Fourth, we addressed whether there is a positive relationship between promiscuity and survival in cooperative species, and how this differs from the relationship between these two traits in non-cooperative species using two approaches. First, we modelled promiscuity as the response variable (using a binomial distribution with a logit link function) with mass (covariate), survival (covariate) and breeding system (two-level factor: cooperative versus non-cooperative) fitted as fixed effects. We included an interaction between survival and breeding system to test whether the magnitude and/or the direction of the relationship between promiscuity and survival in cooperative species is significantly different from non-cooperative species. Prior to analyses, mass was log-transformed, and both survival and mass were Z-transformed (mean of 0 and standard deviation of 1). Second, we tested whether the correlated evolution of survival and promiscuity through evolutionary time differs between cooperative and non-cooperative species by constructing a multi-response BPMM. We fitted survival and promiscuity as binomial responses and included breeding system (cooperative or non-cooperative) as a fixed effect. To estimate the covariance between survival and promiscuity for cooperative and non-cooperative breeders separately, we estimated a 2×2 covariance matrix for the interaction between phylogeny and trait at the level of each breeding system. This estimates the covariance between survival and promiscuity that arises owing to shared ancestry between species of cooperative and non-cooperative breeders separately. We expect a positive correlation between survival and promiscuity through evolutionary time in cooperative species, whereas a negative correlation has previously been found between survival and promiscuity for non-cooperative species.

We ran each BPMM for 4 100 000 iterations with a burn-in of 100 000 and a 1000 thinning interval as suggested by the mcgibbsit package [45] in R, which combines Raftery and Lewis's run length

diagnostic with Gelman and Rubin's convergence diagnostic [46]. Estimates of parameters were calculated as the mode of posterior samples and their significance was assessed by examining the credible interval: if the 95% CI of the posterior mode spanned zero this indicated the parameter was not statistically different from zero. The convergence of all models was assessed using Gelman diagnostics and by assessing plots of chain mixing as well as levels autocorrelation. We provide annotated R code in the electronic supplementary material.

3. Results

(a) Is reproduction delayed in cooperative breeders?

Reproduction was significantly delayed in cooperative breeders relative to non-cooperative breeders (difference in mean age at first breeding: parameter estimate $\beta = 1.38$, 95% CI = 0.83–1.83; $n_{\text{species}} = 39$) with non-cooperative species having a higher probability of breeding in their first year relative to cooperative breeders (difference in intercepts: $\beta = -3.35$, CI = -5.69 to -1.56 ; $n_{\text{species}} = 39$; figure 1*a,b*). While queuing to become breeders, helpers had little access to direct reproduction, siring less than 8% of young on average (figure 1*c*; proportion of young sired by dominant breeders: $\beta = 0.98$, CI = 0.91–0.99; $n_{\text{species}} = 40$).

(b) Do cooperative breeders live longer than non-cooperative breeders?

Cooperatively breeding species had higher levels of annual survival than non-cooperatively breeding species after controlling for mass, latitude, promiscuity and phylogenetic history (difference in survival: $\beta = 0.41$, CI = 0.20–0.68; $n_{\text{species}} = 238$; figure 2).

(c) Does high survival make the evolution of cooperative breeding more likely?

Our multi-response BPMM revealed a significant positive phylogenetic correlation between survival and cooperation through evolutionary time ($r = 0.53$, CI = 0.26–0.71; $n_{\text{species}} = 238$). This finding was extended by our evolutionary transitions analysis: high survival preceded evolutionary transitions to cooperation as the survival of non-cooperative ancestors that gave rise to cooperative breeders was higher than non-cooperative ancestors that only had non-cooperative descendants (difference in survival: $\beta = 0.32$, CI = 0.01–0.72; $n_{\text{species}} = 238$). Ancestral survival did not differ between non-cooperative ancestors that gave rise to cooperative breeders and cooperative ancestors that only had cooperative descendants, as might be expected if cooperation itself selects for increased survival (difference in survival: $\beta = -0.28$, CI = -0.76 – 0.26 ; $n_{\text{species}} = 238$; figure 3). Finally, a model of correlated evolution between cooperation and survival received more support than one assuming independent evolution of these traits (Bayes factor = 23.53; note that Bayes factors > 10 provide very strong evidence of a difference [44]). Furthermore, a model in which transitions to cooperative breeding were independent of survival received less support than a model in which transitions to cooperative breeding were dependent on survival (Bayes factor = 2.54, positive evidence of a difference), while a model in which survival evolved independently of cooperation was as good as a model in which survival was dependent on

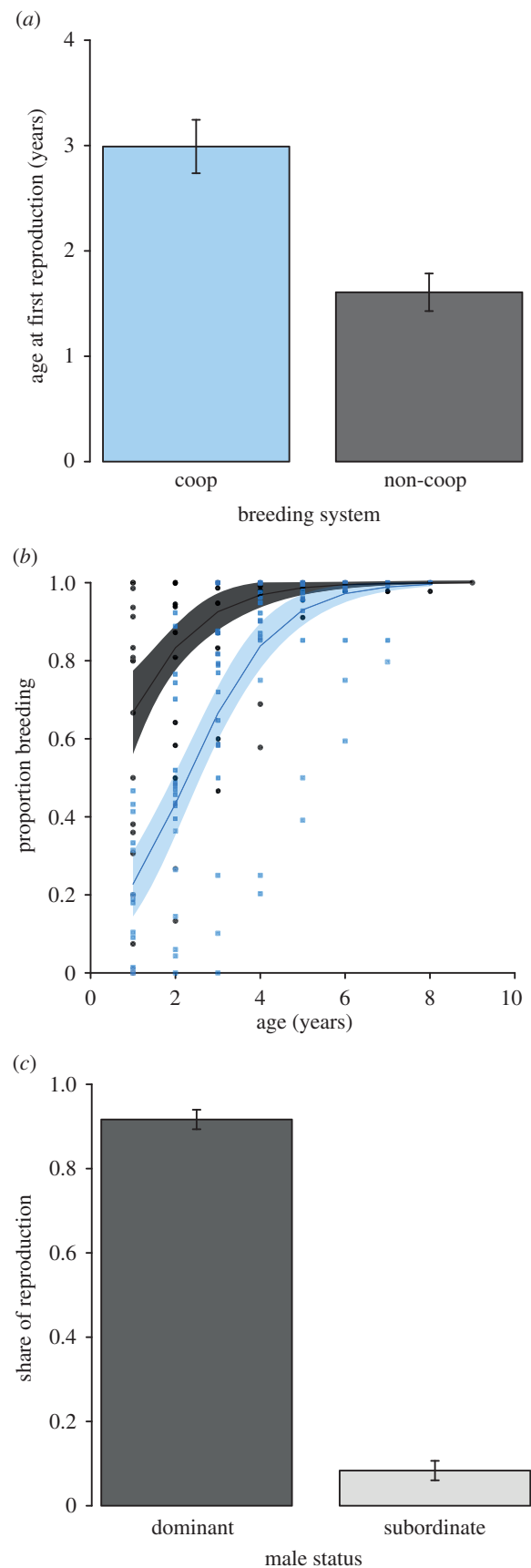


Figure 1. (a) Mean age at first reproduction is later in cooperative breeders than in non-cooperative breeders. Data show mean \pm s.e. ($n_{\text{species}} = 39$). (b) Fewer cooperative breeders (blue/grey, squares) breed in a given age class compared with non-cooperative breeders (black, circles). For each year the proportion of individuals of each species breeding is plotted. Regression lines are presented with 95% CI ($n_{\text{species}} = 39$). (c) Dominant males monopolize reproduction within social groups. Data show mean \pm s.e. ($n_{\text{species}} = 40$).

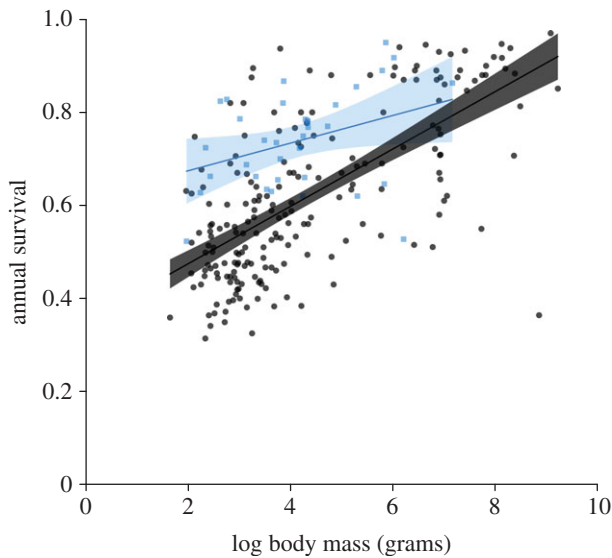


Figure 2. Cooperative breeders (blue/grey, squares) have higher levels of survival than non-cooperative breeders (black, circles). Regression lines are presented with 95% CI ($n_{\text{species}} = 238$). Excluding the wild turkey, *Meleagris gallopavo*, the outlier in the bottom right corner, makes no difference to the result (difference in survival: $\beta = 0.45$, CI = 0.19–0.66).

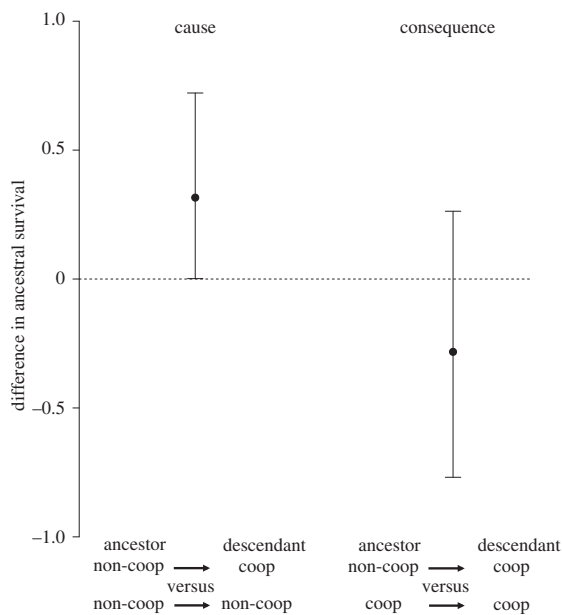


Figure 3. There was a significant difference in survival between non-cooperative ancestors of cooperative descendants and non-cooperative ancestors of non-cooperative descendants: the 95% CI of the estimate does not include zero. By contrast, survival did not differ between non-cooperative ancestors of cooperative descendants and cooperative ancestors of cooperative descendants. Data show mean estimate of difference in ancestral survival \pm 95% CI of the posterior distribution of estimates of the mean.

cooperation (Bayes factor = 0.41, weak evidence of a difference; electronic supplementary material, figure S2). Taken together, these results show that transitions to cooperative breeding are more likely if a species is long lived.

(d) Is long life more pronounced in promiscuous cooperative breeders?

There was a positive relationship between promiscuity and survival in cooperative breeders, whereas this relationship

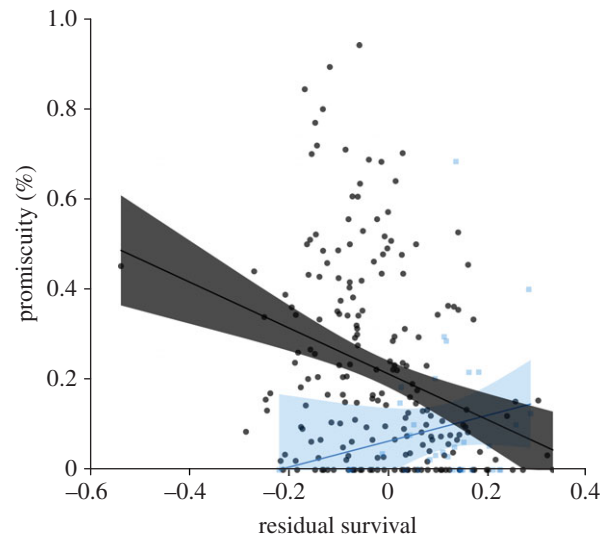


Figure 4. As promiscuity increases among non-cooperative breeders (black, circles) survival decreases while in cooperative breeders (blue/grey, squares) there is an increase in survival as promiscuity increases. Regression lines are presented with 95% CI ($n_{\text{species}} = 238$). Excluding the wild turkey, *Meleagris gallopavo*, the outlier on the left, makes no difference to the result (difference in slopes: $\beta = 1.24$, CI = 0.10–2.32).

was negative in non-cooperative breeders (difference in slopes: $\beta = 1.33$, CI = 0.14–2.37; $n_{\text{species}} = 238$; figure 4). Furthermore, using multi-response BPMMs, we found a negative correlation between survival and promiscuity through evolutionary time in non-cooperative species ($r = -0.51$, CI = -0.72 to -0.19), but no correlation between survival and promiscuity through evolutionary time in cooperative species ($r = -0.22$, CI = -0.79 to 0.44). This demonstrates that while long life is associated with promiscuity in cooperative species, in non-cooperative species, long life is associated with monogamy.

4. Discussion

Our analyses show that the evolution of cooperative breeding in birds is associated with a life-history strategy that is distinct from that of non-cooperative breeders. Young birds living in cooperatively breeding family groups remain on their natal territories and queue for a chance to reproduce. While queuing, opportunities to reproduce are rare, but there are opportunities to increase their indirect fitness by helping to raise related nestmates. Our results suggest that cooperative breeding is more likely to evolve in long-lived species and that high levels of promiscuity are only evolutionarily stable in cooperative societies when individuals are sufficiently long lived to obtain future direct fitness benefits. Conversely, high promiscuity is more likely to undermine the evolution of cooperation in short-lived species because the indirect fitness benefits of helping are relatively low and the costs of forgoing direct reproduction are relatively high.

Building on previous work showing an association between longevity and cooperative breeding in birds [11,13,14], we are now able to distinguish between whether long life is a cause or a consequence of cooperative breeding. We found that long life makes cooperation more likely to evolve by comparing the life spans of the ancestors of cooperative and non-cooperative species, consistent with theoretical models of the evolution of

cooperative breeding. Furthermore, we found no evidence for the alternative prediction that long life evolves as a response to the survival benefits of group living, as has been argued to be the case in cooperatively breeding mammals [47,48].

Recent theoretical and empirical work has emphasized monogamy as an important predictor of transitions to cooperative societies [18–22], yet there are numerous species that do not fit this pattern. The Australian magpie, *Gymnorhina tibicen*, and the superb fairywren, *M. cyaneus*, are well-known examples of promiscuous cooperative species [49,50]. Our results help explain promiscuity in such species. The enhanced direct fitness benefits associated with long life potentially compensate for the costs to a helper's indirect fitness due to promiscuity, making cooperation possible. This is reflected in the striking difference in the relationship between promiscuity and survival in cooperative and non-cooperative species. This shows that the difference in lifespan between cooperative and non-cooperative species occurs at high levels of promiscuity.

An interaction between selection on life-history characteristics and social behaviour is a general expectation from theory that need not apply only to birds. Some species of social insects live in small groups composed of breeders and subordinate helpers, very much like those of cooperatively breeding birds [51–53]. Low levels of relatedness between individuals in these species make direct reproduction the best fitness-maximizing strategy. Similar to our finding in birds, individuals that live longer have a greater possibility of becoming a dominant breeder, which leads to cooperation despite low indirect fitness benefits. For example, in the paper wasp, *Polistes dominulus*, about a third of foundress nest-mates are unrelated to each other, and therefore the potential for indirect fitness benefits from helping to raise the dominant female's young are limited. Unrelated helpers gain direct fitness benefits

instead through the chance of later reproduction via nest inheritance [54]. This reflects how general principles of inclusive fitness theory can explain equivalent phenomena in taxa as divergent as birds and insects.

Overall, our results provide the first comparative evidence that cooperatively breeding birds living in family groups delay reproduction, that helpers have limited opportunities for reproduction during this time and that long life increases the likelihood of cooperative breeding evolving. The association between long life and cooperation seems to arise when two conditions are met. First, options for direct fitness early in life are limited. Second, promiscuity degrades a helper's indirect fitness. It is the combination of these two factors that seems to have previously been overlooked. These results make sense of why promiscuous cooperative species are exceptionally long lived and help to verify some of the assumptions underlying the theory of the evolution of social behaviour and life history.

Data accessibility. The datasets and R code supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. A.S.G. and C.K.C. conceived of the study; P.A.D. designed the study; A.S.G., C.K.C. and P.A.D. collected data; P.A.D. and C.K.C. participated in data analysis; P.A.D., A.S.G. and C.K.C. drafted the manuscript and all authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. P.A.D. was supported by a NERC studentship. C.K.C. was supported by grants from the Swedish Research Council (VR) and by a Wallenberg Academy Fellowship, and A.S.G. by the Royal Society.

Acknowledgements. Many thanks to Stu West and Berti Fisher for useful discussion and comments. We acknowledge the use of the University of Oxford Advanced Research Computing (ARC) facility in carrying out this work (<http://dx.doi.org/10.5281/zenodo.22558>).

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