

Promiscuity and the evolutionary transition to complex societies

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Theory predicts that the evolution of cooperative behaviour is favoured by low levels of promiscuity leading to high within-group relatedness^{1–5}. However, in vertebrates, cooperation often occurs between non-relatives and promiscuity rates are among the highest recorded. Here we resolve this apparent inconsistency with a phylogenetic analysis of 267 bird species, demonstrating that cooperative breeding is associated with low promiscuity; that in cooperative species, helping is more common when promiscuity is low; and that intermediate levels of promiscuity favour kin discrimination. Overall, these results suggest that promiscuity is a unifying feature across taxa in explaining transitions to and from cooperative societies.

The increase in complexity from simple replicating molecules to complex animal societies has involved approximately eight major evolutionary transitions^{6,7}. Almost all of these transitions have required the problem of cooperation to be solved, allowing independently replicating entities to reproduce cooperatively as a group. The problem we address is what causes the transition from independent breeding, where individuals pursue their own selfish interests, to cooperative breeding, where individuals forgo their own reproduction to help others.

It has been proposed^{1,2} that a key factor driving the transition from solitary individuals to complex animal societies is the number of males that a female mates with (the ‘monogamy hypothesis’; Fig. 1). Consider an individual that faces the decision of either dispersing to breed independently or remaining in its family (natal) group to help raise siblings. If the mother of this individual is monogamous (mated with only one male), then the focal individual will share half of its genes with both its potential offspring and its siblings^{3–5} (Fig. 1b). In this case, helping to raise a sibling is equivalent to raising offspring from the point of view of passing genes to the next generation. Any small ecological benefit of cooperation could then tip the balance in favour of helping to raise siblings^{1,2,4,5,8}. In contrast, if the mother of our focal individual mates with multiple males, relatedness to siblings will be lower than relatedness to its own offspring and selection for cooperative breeding will be weaker^{4,5,9} (Fig. 1b).

The monogamy hypothesis has the potential to be of general importance, across all sexually reproducing organisms^{1,2,10}. It builds on kin selection theory to suggest that a single variable, the rate of promiscuity, could have a key role in determining when the evolutionary transition to cooperative animal societies occurs, because of its influence on relatedness (Fig. 1). Support for the monogamy hypothesis comes from analyses of eusocial insects, which have shown that strict lifetime monogamy is the ancestral state of transitions to societies with sterile worker castes¹¹. However, the irreversible evolution of sterile castes has occurred in very few species—it is more commonly the case that non-breeding helpers retain reproductive potential. To understand evolutionary transitions to cooperative

societies more generally, the challenge is to test whether promiscuity rates explain why an individual with the potential to breed chooses to help instead.

There are a number of reasons why monogamy may be less important in the evolution of cooperative breeding in vertebrates. First, direct benefits of cooperation that increase reproductive success and do not depend on kinship have been suggested to have a greater role in vertebrates^{12–14}. Second, strict lifetime monogamy is relatively rare in vertebrates. Two of the highest promiscuity rates ever recorded are in cooperative breeders: the superb fairy-wren, *Malurus cyaneus*, and the Australian magpie, *Gymnorhina tibicen* (Supplementary Information). Third, it has been argued that cooperative breeding will actually lead to higher rates of promiscuity, because helpers release females from the need to secure paternal care from her mate through paternity assurance¹⁵.

We exploit the extensive literature on birds to test whether rates of female promiscuity have influenced the evolutionary transitions to and from cooperative breeding. Specifically, we use promiscuity data to compare the potential kin-selected benefits of helping across bird species, and ask whether this helps explain the distribution of cooperative breeding. There is wide unexplained diversity in both promiscuity and cooperation across bird species^{12,13,16–19} (Fig. 2). We collected

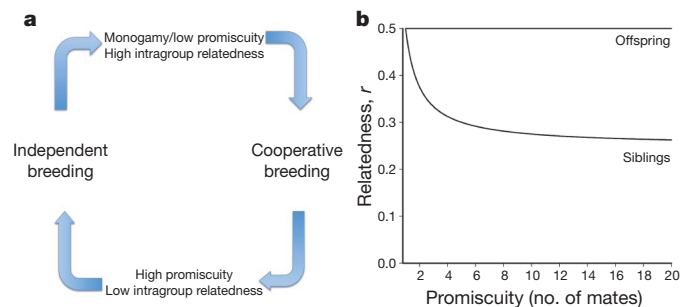


Figure 1 | The monogamy hypothesis. **a**, Monogamy, or low levels of promiscuity, leads to high relatedness in family groups that favours the transition to cooperative societies (increasing the relatedness term, r , in Hamilton's rule³, which states that cooperation will be favoured if $rb > c$, where b is the benefit in terms of reproductive success to the recipient of aid and c is the cost to the performer of a cooperative behaviour). High levels of promiscuity lead to a low relatedness in family groups that favours the loss of cooperative breeding. **b**, Promiscuity and relatedness. Female promiscuity (number of mates) is plotted against the mean genetic relatedness between potential helpers and either their siblings or their offspring. An individual is always related to its offspring with $r = 0.5$. In contrast, as the number of males its mother mates with increases, the relatedness to siblings decreases from $r = 0.5$ to $r = 0.25$ (full-siblings to half-siblings). Across 11 species of cooperative breeders, we found this expected negative relationship between helper–offspring relatedness and female promiscuity (Supplementary Fig. 1).

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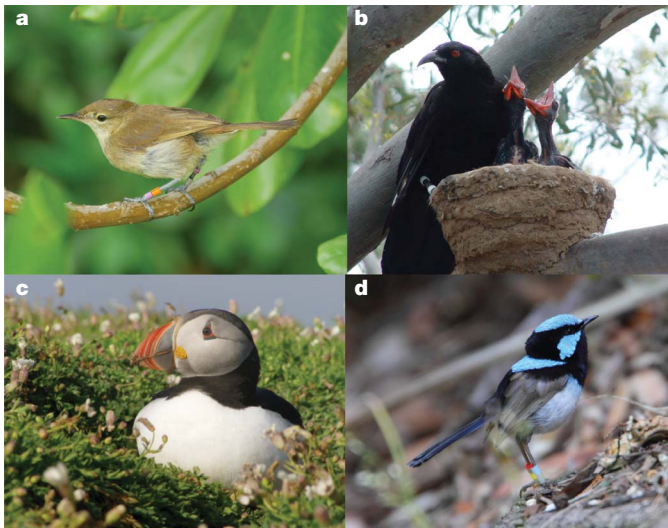


Figure 2 | Making sense of the diversity. Helping may be facultative, as in the Seychelles warbler, *Acrocephalus sechellensis*²⁸ (a), or obligate: the chicks in the nest of the white-winged chough, *Corcorax melanorhamphos* (b), have no chance of survival if their parents do not receive assistance from helpers. Promiscuity can be high in cooperative breeders but low in species without cooperative care—cooperative breeding is unknown in seabirds such as the puffin, *Fratercula arctica* (c), which are either strictly monogamous or have extremely low rates of promiscuity. In contrast, the superb fairy-wren, *Malurus cyaneus* (d), is a cooperative breeder with one of the highest extra-pair paternity rates ever recorded¹⁵. To make helping pay, the benefits have to outweigh the costs of breeding independently, and this depends on ecological as well as genetic factors. (Photos courtesy M. Hammers (a), N. Beck (b), S. Patrick (c), G. Dabb (d).)

available data on promiscuity rates in birds (267 species) and defined species as either cooperative or non-cooperative depending on the presence of non-breeding helpers in family groups (Supplementary Table 15).

Consistent with the monogamy hypothesis, we found that the level of promiscuity (the percentage of broods in the population containing one or more extra-group offspring; Supplementary Information) was significantly lower in cooperatively breeding species (Fig. 3a and Supplementary Table 2). Overall, promiscuity rates were three times greater in non-cooperative species than in cooperative species (Bayesian phylogenetic mixed model²⁰ (BPMM): cooperative: $N_{\text{species}} = 35$, parameter estimate (β) = 0.05, credible interval (CI) = 0.02 to 0.17; non-cooperative: $N_{\text{species}} = 232$, $\beta = 0.15$, CI = 0.05 to 0.30; $P = 0.004$; Fig. 3a and Supplementary Tables 2 and 3).

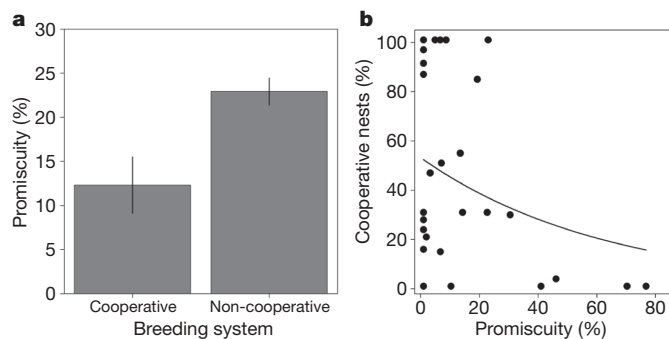


Figure 3 | Promiscuity and cooperation. a, Rates of promiscuity (percentage of broods with one or more offspring sired by an extra-group male) in cooperative and non-cooperative species. Promiscuity was significantly higher in non-cooperative than in cooperative species (Supplementary Tables 2 and 3). Data shown, mean \pm s.e. b, The relationship between levels of cooperation (population with the lowest percentage of nest with helpers throughout the species range) and promiscuity in cooperative species. Helpers were present in a lower percentage of nests in species with higher rates of promiscuity (Supplementary Table 9). The line is the log-linear regression curve.

Although these results are consistent with the monogamy hypothesis, they do not demonstrate that the transition to cooperative breeding is more likely to occur in less promiscuous species. To test this prediction, we examined whether cooperative breeding and promiscuity are correlated through evolutionary time and found support for the predicted negative correlation (multi-response BPMM²⁰: $r = -0.63$ (phylogenetic correlation), CI = -0.86 to -0.33 , $P = 0.001$, Supplementary Table 5; continuous-time Markov models of correlated versus independent evolution²¹: $P = 0.02$, Supplementary Table 6).

As well as predicting transitions to cooperative breeding, the monogamy hypothesis predicts that transitions from cooperative to non-cooperative breeding will be more likely in more promiscuous species. In the species that we examined, cooperative breeding evolved 33 times and has been lost 20 times (Fig. 4a). Examining transitions to cooperative breeding, we found that promiscuity was lower in non-cooperative ancestors of cooperative breeders than in non-cooperative ancestors of non-cooperative species (BPMM: cooperative: $\beta = 0.01$, CI = 0.001 to 0.08; non-cooperative: $\beta = 0.19$, CI = 0.07 to 0.34; $P = 0.001$; Fig. 4b and Supplementary Table 7). Furthermore, the rate of transition to cooperative breeding was over twice as high for ancestors with low promiscuity as for ancestors with high promiscuity (Supplementary Table 6). Examining the loss of cooperative breeding, we found that cooperative ancestors of non-cooperative species tended to be more promiscuous than cooperative ancestors of only cooperative species, but this result was not significant (BPMM: cooperative: $\beta = 0.02$, CI = 0.005 to 0.16; non-cooperative: $\beta = 0.08$, CI = 0.01 to 0.24; $P = 0.07$; Fig. 4b and Supplementary Table 7). Overall, these results show that transitions to cooperation were associated with low promiscuity, and suggest that increases in promiscuity have led to the breakdown of cooperation (Fig. 4b, c).

Although our results show that high levels of promiscuity favour the loss of cooperative breeding, there are many promiscuous, cooperative species (Supplementary Table 15). However, relatedness between helpers and beneficiaries can be increased by kin discrimination (directing aid preferentially towards relatives^{1,3,22} (Supplementary Information)). There is no evidence to suggest that birds are able to discriminate kinship between chicks in a brood using genetic cues, but there is evidence to suggest they can discriminate kinship between broods, using behavioural cues such as vocalizations and breeder turnover^{16,23,24}. By measuring promiscuity as the percentage of nests containing extra-group young, we can make predictions about the strength of selection for kin discrimination across species with different levels of promiscuity. When promiscuity rates are very high or very low, variance in relatedness between broods will be low and we predict that selection to adjust helping effort with respect to kinship will be relatively weak^{23,24}. In contrast, with intermediate levels of promiscuity, variation in relatedness will be highest and we predict that selection for kin discrimination will be greater. This prediction was supported by our data, as we found a dome-shaped relationship across species between the strength of kin discrimination and promiscuity rates ($N_{\text{species}} = 15$, $\beta = -0.31$, CI = -0.67 to 0.01, $P = 0.03$; Fig. 5 and Supplementary Tables 8 and 15).

Promiscuity is also predicted to influence the frequency of cooperation in cooperative breeders. Although we have treated all cooperative breeders equally in the above analyses, the extent of cooperation varies across species. In some species, such as the white-winged chough, *Corcorax melanorhamphos*, reproductive success is completely dependent on the presence of helpers, whereas in other species cooperation seems to be facultative, with some pairs breeding successfully without helpers (Supplementary Table 15). As promiscuity increases, a greater ecological benefit is required for kin selection to favour cooperation, so we predict that the presence of helpers will be less frequent in more promiscuous cooperative species^{1,2,4,5}. In agreement with this, we found that more promiscuous cooperative breeding species had a lower percentage of nests attended by helpers

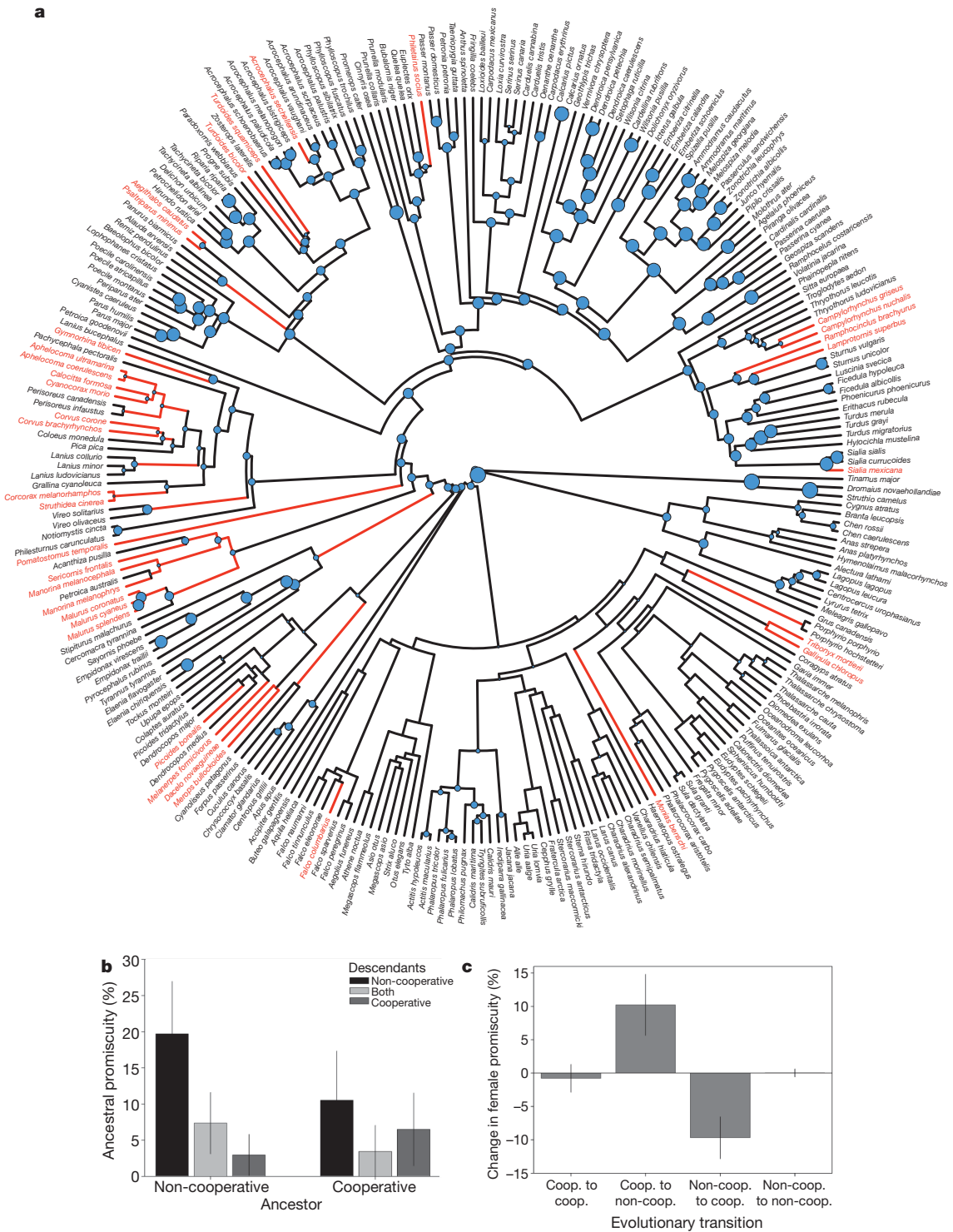


Figure 4 | Promiscuity and the transition to and from cooperative breeding. **a**, The phylogenetic distribution of cooperative breeding and ancestral rates of female promiscuity. Red species labels and branches represent cooperative breeding, and black species labels and branches indicate non-cooperative species. Blue circles indicate ancestral values of rates of promiscuity (larger circles correspond to higher promiscuity). *Petroica* are a poorly constrained group and have been split in the phylogeny. The resulting transitions make no difference to the results (Supplementary Tables 11–14). **b**, Promiscuity in non-cooperative and cooperative ancestral species that gave rise to only non-cooperative descendants (black bars), only ($N_{\text{species}} = 30, \beta = -0.15, \text{CI} = -0.29 \text{ to } -0.02, P = 0.01$; Fig. 3b and Supplementary Table 9).

Overall, our results support the hypothesis that promiscuity is a unifying explanatory variable in the transition to cooperative societies

cooperative descendants (dark-grey bars), or both non-cooperative and cooperative descendants (light-grey bars). Non-cooperative ancestors that lead to cooperative descendants had lower promiscuity than those that produced non-cooperative descendants (Supplementary Table 7). Similarly, cooperative ancestors that produced non-cooperative descendants were more promiscuous than those that produced cooperative descendants (Supplementary Table 7). **c**, The changes in promiscuity associated with transitions to and from cooperative breeding. Rates of promiscuity decreased during transitions to cooperation, but decreased when cooperation broke down. Data shown, mean \pm s.e. of ancestral values.

across species, linking research on kin selection and sexual selection². However, our results also demonstrate how differences between taxa influence the consequences of promiscuity. In eusocial insects, multiple mating is a derived state, evolving after the appearance of sterile

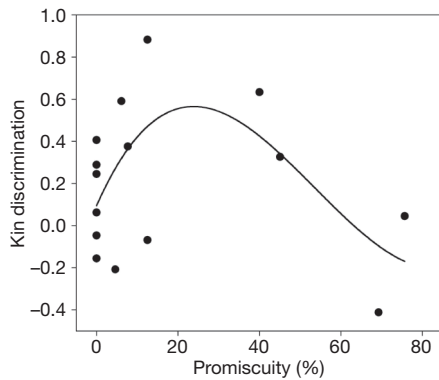


Figure 5 | Kin discrimination and rates of promiscuity. There was a significant quadratic relationship between kin discrimination (correlation between relatedness and help provided) and promiscuity (measured as in Fig. 3a), indicating that kin discrimination was strongest in species with intermediate rates of promiscuity (Supplementary Table 8).

castes, and has not led to the loss of eusociality^{1,2,11,25}. In contrast, high promiscuity can lead to the complete or partial loss of cooperative breeding in birds. This effect may be ameliorated by kin discrimination, which increases average relatedness between helpers and beneficiaries, and can thereby stabilize cooperation even when females mate with multiple males (Figs 3b, 4b and 5). More generally, our results provide empirical support for E. O. Wilson's statement that "sex is an antisocial force in evolution"²⁶ by showing how promiscuity reduces relatedness and hence disrupts selection for cooperation in family groups.

METHODS SUMMARY

We collected data on female promiscuity and whether species were cooperative or non-cooperative breeders from literature searches (Supplementary Information). Our definition of cooperative breeding excluded polyandrous species such as the dunnock, *Prunella modularis*, where an additional breeding adult may attend the nest²⁷ (Supplementary Information), as the monogamy hypothesis only makes predictions about transitions to cooperation in family groups^{1,2}. We carried out our analyses using BPMMs with Markov chain Monte Carlo estimation²⁰ using 'MCMCglmm' in R, version 2.10.1 (see Methods for all software references).

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to A.S.G. (ashleigh.griffin@zoo.ox.ac.uk).

METHODS

Data collection and the phylogenetic tree. Data on extra-group paternity. All species used in the analyses are listed in Supplementary Table 15 and we use Latin names listed in the International Ornithological Congress master list, version 2.3 (December 2009; <http://www.worldbirdnames.org/>). We searched for all published data on extra-pair paternity data in birds by entering the following search terms into the Web of Science (http://thomsonreuters.com/products_services/science/science_products/a-z/web_of_science) on 18 March 2010: keywords “extra-pair paternity OR extra pair paternity OR extra-pair fertilization OR extra pair fertilization OR extra-pair fertilization OR extra pair fertilization OR extrapair”; title “parentage” AND topic “birds”; title “mating system” AND “birds”; all references that cite refs 29, 30, which are major reviews on extra-pair paternity in birds. Two statistics on female promiscuity are frequently published and are highly correlated: the percentage of chicks fathered by extra-pair fathers and the percentage of broods with one or more extra-pair chicks ($r = 0.93$, $N = 272$, $P < 0.0001$).

We collected data on the percentage of broods in the population containing extra-group offspring (hereafter referred to as female promiscuity), as this provides a population-wide measure of the level of female promiscuity. Furthermore, we choose to use extra-group paternity rather than extra-pair paternity for cooperative species, as this removes the possibility of the results being influenced by individuals gaining parentage in the nest where they were helping. In species without a pair bond—for example species without male care, lekking species and parasitic species—we used data on the proportion of nests containing chicks fathered by more than one male.

When there were multiple studies presenting data on promiscuity for a single species, we calculated the mean value of all studies weighted by sample size for use in subsequent analyses (Supplementary Table 15). In cases where we found multiple papers presenting the same set of paternity data, from the same study population and over the same years, to avoid duplication we used information from only one of these papers to calculate the species mean.

We collected data on 280 species. However, for 7 species only estimates of the number of extra-group offspring were available (that is, no data were available on the number of broods with extra-group paternity), and for 6 species the number of broods analysed for paternity were not reported. Therefore, we included 267 species in our analyses. To verify that excluding species did not change our results, we also analysed data on all species ($N = 276$), which gave almost identical results (Supplementary Tables 2 and 3). Of the 267 species used in our analyses, 13 species were not in the supertree. However, for all 13 species there was a congener in the supertree that was not already in our data set. We therefore set the position of the 13 missing species in the supertree to their closely related congeners.

Data on breeding system. We categorized species as either cooperative or non-cooperative. There is a wide diversity of cooperative care for offspring in birds; however, the monogamy hypothesis makes predictions specifically about selection to help in family groups. Therefore, we only classed species as cooperative if helpers did not breed or had zero-to-limited opportunities to breed; typically, these helpers would be retained natal. This definition of cooperative breeding discounts many polyandrous species that are often thought of as ‘cooperative breeders’, such as dunlocks and the Galapagos hawk²³ (Supplementary Table 15). We did not define species as cooperative unless there were helpers present in at least 10% of the nests in any part of their range^{31,32}; neither did we define species as cooperative if there was only limited or anecdotal evidence of helpers being present or if the breeding status of helpers was ambiguous. That said, very few of the species classed as non-cooperative fall into this grey area; an example is the buff-breasted wren (Supplementary Table 15). Species were classified blind as cooperative or non-cooperative, without knowledge of extra-group paternity data. We researched all species in our cooperative breeder set, to determine the breeding status of helpers. Often the most accurate information (using genetic markers) came from the paternity studies we used to measure promiscuity, but we also researched species more widely to obtain a general picture of the breeding system for each species; additional sources of information used are cited in Supplementary Table 15.

Classifying species as either cooperative or non-cooperative is inevitably crude, as in our set of cooperative breeders there is a wide diversity of breeding system—some species, such as the apostlebird and the white-winged chough, are obligate cooperative breeders (never known to reproduce successfully without helpers), whereas others are only cooperative in certain areas of their range, for example the carrion crow. We sought to capture some of this diversity by searching the literature for data on the percentage of nests with helpers for each cooperative breeder in our data set. We aimed to determine the upper and lower limits on the proportion of nests with helpers, throughout a species range, and a point estimate for the study population used in each study from which we extracted data on paternity (Supplementary Table 15). We found the most informative of these measures to be the lower limit, as this clearly distinguishes between facultative and obligate cooperative breeders.

Data on relatedness and kin discrimination. We analysed how promiscuity affected the strength of kin discrimination and the relatedness between helpers and breeders in cooperative species. First, we measured the strength of kin discrimination for each of the cooperative breeders in our data set for which this data was available. This measure captures the extent to which helpers in a species preferentially direct aid towards related young. Specifically, we measured the effect size (r) of relatedness on either the probability of becoming a helper or the amount of help provided. Second, we collected genetic data on the relatedness between helpers at the nest and breeders. Further details on how this data were collected are described in refs 22, 23.

Avian supertree. Full details of the avian supertree we used for our analyses will be published elsewhere (K.E.D. and R. D. M. Page, submitted), so here we describe the methods in brief. The supertree was created from a total of 966 bird trees published between 1976 and 2008 and covering 6,219 species. The supertree was created using the Imperial College supercomputer CX2. CX2 is an SGI ICE 8200EX with 122 nodes. Each node has two quad-core 2.93-GHz Intel X5570 (Nehalem) processors and 24 GB of RAM. The analysis was run on 64 cores over 72 h using TNT³³ with the option `xmult level = 10`, an aggressive search strategy devised to find the shortest trees in as little time as possible. TNT found a single MPT of length 26,242.

We pruned the full supertree (6,219 species) to include only species for which we had data on female promiscuity (267 species), which we then used for all analyses.

Statistical analyses. General techniques. We used BPMMs with Markov chain Monte Carlo estimation using ‘MCMCglmm’²⁰ in R, version 2.10.1³⁴. Flat non-informative priors with a uniform low degree of belief across all parameters were set in all analyses (for specific details see Supplementary Information). Residual variance cannot be calculated for binary traits, and in analyses of binary traits (for example cooperation: 0 = non-cooperative, 1 = cooperative) residual variance was therefore fixed to 1 (ref. 35). Parameter estimates reported are modes from the posterior distribution with 95% lower (lower CI) and upper (upper CI) credible intervals. Reported P values testing differences between levels (for example non-cooperative versus cooperative breeders) are the numbers of iterations when one level is greater or less than the other divided by the total number of iterations. Reported P values for correlations (for example between promiscuity and the probability of being a cooperative breeder) are the numbers of iterations where the correlation is greater or less than zero divided by the total number of iterations.

We examined the convergence of models in three ways using the ‘coda’ R package³⁶. First, we used the run length diagnostic of ref. 37 to estimate the burn-in period and total run length for all parameters in each analysis. Second, we used the diagnostics of refs 38, 39 to assess the convergence of each analysis. The convergence diagnostic of ref. 38 calculates z -scores from mean parameter estimates plus/minus standard errors generated from the first 10% and the last 50% of the chain³⁸. If z -scores follow an asymptotically standard normal distribution, the samples are considered to be drawn from a stationary distribution³⁸. The diagnostic of ref. 39 examines whether the sampled output comes from a stationary distribution, using the Cramér/von Mises test. Third, we examined plots of the sampled output to check visually that the chain had mixed properly. Testing how promiscuity influences the evolution of cooperation. We performed six analyses to examine how promiscuity influences the evolution of cooperative breeding.

(1) Testing the relationship between promiscuity and the relatedness between potential helpers and breeders. We tested whether relatedness between breeders and potential helpers (response variable) across cooperative breeding species was negatively related to female promiscuity (explanatory variable) using BPMMs with a binomial distribution and a logit link function (Supplementary Fig. 1). We ran two analyses. First, we analysed the relationship between relatedness and female promiscuity treating species as independent data points (Supplementary Table 1). Second, we repeated the analysis taking into account the phylogenetic relationships between species by specifying a phylogenetic covariance matrix (see refs 20, 35 for details).

(2) Testing the association between cooperative breeding and promiscuity. We tested whether female promiscuity (response variable) was lower in cooperative species compared to non-cooperative species (explanatory variable) using BPMMs with a binomial distribution and a logit link function (Supplementary Table 2). We accounted for differences in samples sizes between studies by analysing female promiscuity (response variable) as the total number of broods with one or more extra-group offspring versus the number of broods with only within-group chicks, rather than analysing percentages, which disregard sample sizes. We ran all analyses twice, once treating species as independent data points and once taking into account phylogenetic relationships between species.

(3) Phylogenetic tests of correlated evolution between cooperative breeding and promiscuity. We tested whether there was a negative phylogenetic correlation

between female promiscuity and cooperative breeding using multi-response BPMMs. We fitted the probability of being cooperative (0 = non-cooperative, 1 = cooperative) as a binary response and the rate of female promiscuity (number of broods with extra-group chicks versus number of broods with only within-group chicks) as a binomial response. To establish the strength of the correlation between the evolution of cooperation and levels of female promiscuity, three analyses were performed. First, we analysed species as independent data points, allowing the phenotypic correlation between cooperation and female promiscuity to be estimated (Supplementary Table 4). Second, we estimated the phylogenetic correlation between the two variables by specifying an unstructured phylogenetic variance–covariance matrix for the two traits (MCMCglmm code = us(trait): animal)^{20,35} (Supplementary Table 5). This estimates variance attributable to phylogenetic history in both traits and the covariance between the traits that arises owing to shared ancestry between species. These techniques are analogous to those used in quantitative genetics to estimate genetic correlations between traits through pedigrees^{20,35}. Finally, we fitted a phylogenetic variance–covariance matrix for the two traits but constrained the phylogenetic covariance between cooperation and female promiscuity to be zero (MCMCglmm code = idh(trait): animal), therefore assuming independent evolution of the two traits^{20,35}. We then compared the deviance information criteria (DIC³⁵) of the model estimating correlated evolution between the traits with the analysis where the evolution of cooperation and female promiscuity were assumed to be independent.

(4) The influence of female promiscuity on transitions to and from cooperation. We tested whether evolutionary transitions to and from cooperative breeding were associated with different levels of female promiscuity in two different ways.

First, we used the BayesTraits^{21,40} DISCRETE module with maximum-likelihood estimation to estimate transition rates to and from cooperative breeding under high and low levels of promiscuity. DISCRETE can only examine transitions between binary traits and therefore we classified female promiscuity as low (less than or equal to the median) or high (greater than the median). We tested whether models allowing correlated evolution of cooperative breeding and female promiscuity had a significantly higher log likelihood than models assuming independent evolution of traits, using log-likelihood ratio tests⁴⁰ with degrees of freedom equal to the difference in the number of parameters estimated (Supplementary Table 6). Furthermore, using log-likelihood ratio tests we tested whether individual transition rates were significantly different from zero, comparing models where individual transition rates were restricted to zero with models where transition rates were estimated^{21,40}.

Second, because of the restrictions of having to use binary traits in DISCRETE, we examined whether transitions to and from cooperative breeding were influenced by female promiscuity using a different approach. Using data on whether species were cooperative or non-cooperative (response variable), we reconstructed states of cooperation for ancestral species using a BPMM with 7,100,000 iterations, 100,000 burn-in iterations and a thinning interval of 1,000 iterations²⁰. For each node, this gave posterior modes of being non-cooperative or cooperative. For all nodes, the posterior modes were either greater than 0.9999, and were classed as cooperative, or less than 0.0001, and classed as non-cooperative. Furthermore, the model correctly predicted cooperative and non-cooperative breeding for all contemporary species. This analysis revealed that there were 33 transitions from non-cooperative to cooperative breeding and 20 transitions from cooperative to non-cooperative breeding.

We used the information from ancestral reconstruction of cooperative breeding to classify nodes of the tree according to the descendant species they gave rise to, which fell into the following categories: (i) non-cooperative nodes that gave rise to only non-cooperative direct descendants; (ii) non-cooperative nodes that gave rise to both non-cooperative and cooperative direct descendants; (iii) non-cooperative nodes that gave rise to only cooperative direct descendants; (iv) cooperative nodes that gave rise to only non-cooperative direct descendants; (v) cooperative nodes that gave rise to both non-cooperative and cooperative direct descendants; (vi) cooperative nodes that gave rise to only cooperative direct descendants. We analysed whether classifications (i)–(vi) (explanatory variable) were associated with differences in female promiscuity (response variable), to test whether transitions to and from cooperative breeding were preceded by differences in female promiscuity. Although data on female promiscuity is only available for the tips of the tree, phylogenetic mixed models allow ancestral values for female promiscuity to be estimated and it is therefore possible to test whether there were differences in female promiscuity among categories (i)–(vi) (Supplementary Table 7).

(5) Meta-analysis of promiscuity and kin discrimination. Finally, we tested whether female promiscuity was related to the strength of kin discrimination in cooperative species using a random-effects Bayesian phylogenetic meta-analysis²⁰. We analysed variation in the effect size of kin discrimination (response

variable, z -transformed) in relation to female promiscuity (explanatory variable) and weighted each data point by the inverse variance associated with each study, which we approximated by $1/(n - 3)$ where n is the sample size of the study⁴¹. We again ran the analysis twice, once treating species as independent data points and once taking into account phylogenetic relationship between species (Supplementary Table 8).

(6) Female promiscuity and levels of cooperation. We tested whether variation in the percentage of cooperative nests (binomial response variable) was negatively correlated with levels of promiscuity (explanatory variable) using a BPMM. We ran the analysis twice, once treating species as independent data points and once taking into account phylogenetic relationships between species (Supplementary Table 9).

Variables confounding the relationship between promiscuity and cooperation. There are variables that correlate with both promiscuity and cooperative breeding and may therefore potentially confound any relationship between cooperative breeding and promiscuity. Two of the most widely established variables that correlate with both cooperative breeding and promiscuity are longevity and breeding range^{19,29,30}. We checked whether the relationship between cooperative breeding and female promiscuity was still present after controlling for these variables.

First, we gained data on species longevity from The Animal Ageing & Longevity Database⁴² (<http://genomics.senescence.info/species/>). We were able to obtain information on the maximum longevity for 184 species (16 cooperative, 168 non-cooperative) for which we had data on female promiscuity and cooperative breeding. We found that the difference in female promiscuity between cooperative and non-cooperative species was not confounded by longevity; in fact, the negative relationship between cooperative breeding and promiscuity was stronger after controlling for variation in longevity (BPMM of female promiscuity (response variable) with breeding system (cooperative and non-cooperative) and longevity (covariate) as fixed effects (posterior mode (95% CI): cooperative breeders = 0.01 (0.002, 0.15) versus non-cooperative breeders = 0.12 (0.04, 0.43), $P = 0.001$; longevity = -0.02 (-0.05 , 0.03), $P = 0.26$).

Second, cooperative breeders tend to be more prevalent nearer the equator, where female promiscuity tends to be lower³⁰. We therefore tested whether any differences in female promiscuity between cooperative and non-cooperative breeders were influenced by latitude by entering breeding range, as listed in the International Ornithological Congress master list, version 2.3, as an explanatory variable (fixed factor). We found that the relationship between promiscuity and cooperation still remained even after controlling for breeding range (BPMM of female promiscuity (posterior mode (95% CI): cooperative breeders = 0.08 (0.03, 0.33) versus non-cooperative breeders = 0.23 (0.09, 0.60), $P = 0.002$; DIC of model including breeding range = 19115.1; DIC of model excluding breeding range = 19124.1).

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