Comparative Analyses of Cooperative Breeding in Birds

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Declaration

I declare that this thesis was composed by myself and that the work contained herein is my own except where explicitly stated in the text. The work has not been submitted for any degree or professional qualification except as specified.

Philip Downing, Trinity 2016

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Ashleigh, thank you for giving me the freedom to pursue crazy ideas, to make endless mind maps and for your patience. It's been a privilege to learn with you. Charlie, thanks so much for your support over the last few years and for sharing your intimidating statistical knowledge. See you in Lund!

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I dedicate this thesis to my mum, Karen. Thanks for everything.

Contributions and Publications

The following publications have arisen from this thesis and are presented in chapters 2 and 3 respectively:

- Downing, P. A., Cornwallis, C. K. & Griffin, A. S. (in press) How to make a sterile helper. *BioEssays*.

I designed the study, formulated the hypothesis, prepared the figures and collected the data. Ashleigh Griffin and Charlie Cornwallis contributed to developing the ideas presented in the manuscript and all co-authors commented on the manuscript (33% each).

- Downing, P. A., Cornwallis, C. K. & Griffin, A. S. (2015) Sex, long life and the evolutionary transition to cooperative breeding in birds. *Proceedings of the Royal Society B*, 282: 20151663.

Ashleigh Griffin, Charlie Cornwallis and I conceived of the study (33% each). I designed the study and collected the data. Charlie Cornwallis helped with data analysis (40%) and I prepared the figures. All co-authors contributed to the interpretation of the results and commented on the manuscript (33% each).

Chapter 4 is in review at the *American Naturalist*:

- Downing, P. A., Cornwallis, C. K. & Griffin, A. S. Sex Differences in Helping in Cooperative Societies are Explained by Future Direct Fitness Benefits. *American Naturalist* (in review).

Ashleigh Griffin and I conceived of the study (50% each). I designed the study and collected the data. Charlie Cornwallis helped with data analysis (20%) and I prepared the figures. All co-authors contributed to the interpretation of the results and commented on the manuscript (33% each).

Chapters 5 is being prepared for publication. Ashleigh Griffin, Charlie Cornwallis and I conceived of and designed the study (33% each). I collected the data. Charlie Cornwallis helped with data analysis (50%) and I prepared the figures. Ashleigh Griffin, Charlie Cornwallis and I wrote the manuscript (33% each).

Chapter 6 is my own work.

In addition, I have contributed to two other projects:

- Farine, D. R, Downing, C. P. & Downing, P. A. (2014) Mixed-species associations can arise without heterospecific attraction. *Behavioral Ecology*, 25: 574-581.
- Cornwallis, C. K., Botero, C. A., Rubenstein, D. R., Downing, P. A., West, S. A. & Griffin, A. S. (2017) Cooperation facilitates the colonization of harsh environments. *Nature Ecology and Evolution*, 1: 0057.

These are included in appendices A and B respectively.

Abstract

In cooperatively breeding species, groups of three or more individuals cooperate in raising young. The challenge is to explain why investing in another individual's reproduction is a better strategy for transmitting genes to future generations than breeding independently. Theoretically, individuals cooperate either because it increases their own reproduction (direct fitness) or because it increases the reproductive success of relatives with whom they share genes (indirect fitness). Life history and demographic parameters are expected to influence the direct and indirect fitness benefits of cooperating. However, how these parameters shape the evolution of cooperative breeding remains largely unexplored. In this thesis, I develop our understanding of the role of life history and demographic parameters in the evolution of cooperative breeding using birds as a model system. Specifically: 1) I review the role of longevity in the evolution of cooperative breeding; 2) I demonstrate that long life makes the evolution of cooperative breeding more likely, supporting a theoretical prediction that territory inheritance is an important incentive for helping behaviour; 3) I show that female helpers invest more in raising siblings than male helpers when they have a higher probability of breeding in their natal group, which suggests that future breeding opportunities shape investment in helping as relatedness of male and female helpers to their siblings is equal; 4) I show that ancestral polyandry only influences the likelihood of cooperative breeding evolving in family groups, not in non-family groups, and that there is a reproductive division of labour in family groups while non-family groups are smaller and consist of co-breeders; 5) Finally, I test whether breeders adjust their investment in parental behaviour when they have helpers at the nest in response to the reproductive costs of care.

Contents

Foreword

I have not provided a detailed review of the literature in the introduction as each subsequent chapter contains its own review of the relevant topics. To save trees, all supplementary information mentioned in the text, including data tables, figures and R scripts, can be accessed online at: http://philipdowning.weebly.com/research.

“*Insect sociality is just the visible tip of an iceberg of cooperation.*”

David Queller, 1997

Chapter 1

Introduction

Social Behaviour

Social behaviours are those which affect the fitness of the individual that performs the behaviour and another individual (West *et al.*, 2007). These are observed across the domains of life, ranging from chemical warfare in single-celled prokaryotes to cooperative colony founding in social wasps (Queller *et al.*, 2000; Riley *et al.*, 2003; Ghoul *et al.*, 2015). Social behaviours can be categorised according to their fitness consequences for the actor (the individual that performs the behaviour) and the recipient (the individual affected by the behaviour of the actor) (Hamilton, 1963; 1964a; 1964b; West *et al.*, 2007). Fitness consequences have either a positive or a negative effect on actor and recipient, resulting in four types of social behaviour (actor/recipient): mutual benefit (+/+), altruism (–/+), selfishness (+/–) and spite (–/–). Mutual benefit and altruism are cooperative behaviours because they provide a fitness benefit to the recipient (West *et al.*, 2007).

Hamilton (1963) noted that altruism presents a problem for the classical theory of natural selection. An organism that behaves in a way that benefits another at its own expense will have a lower representation of its genes in the next generation. Instead natural selection will favour selfish individuals who do not pay this cost. To explain the evolution of altruism, Hamilton partitioned natural selection into direct and indirect components (Hamilton, 1964a; b). Direct fitness is that gained through the impact of an individual's behaviour on her own offspring. Indirect fitness is that gained through an individual's behaviour on the offspring of others (Grafen, 1984). In doing so, Hamilton not only provided an explanation for altruism but generalised Darwinian fitness to take social interactions into account, demonstrating that organisms act as if maximising their inclusive fitness, the sum of direct and indirect fitness components (Grafen, 1984; West & Gardner, 2013).

BOX 1. Cooperative Breeding

Cooperative breeding systems are those in which groups of three or more individuals cooperate in raising young. This definition includes multiple breeding systems:

- **Helping at the Nest** – *groups are families formed through the retention of offspring*
- **Redirected Helping** –*failed breeders help at the nest of a relative*
- **Plural Breeding** – *groups contain more than one breeding female*
- **Communal Breeding** – *females pool young and cooperate in brood care*
- **Cooperative Polyandry** – *groups in which there is shared paternity*

Rather than treating each of these breeding systems separately, I have chosen to split cooperatively breeding species into family groups (*helping at the nest* and *redirected helping*) and non-family groups (*plural breeding*, *communal breeding* and *cooperative polyandry*). This is because kin selection can only operate if groups consist of related individuals (Bourke, 2011). We therefore expect different selection pressures to favour cooperation in family and non-family groups and for helping to be altruistic in family groups but mutually beneficial in non-family groups.

Cooperative Breeding Allows us to Test Inclusive Fitness Theory

Cooperatively breeding species, those in which groups of three or more individuals cooperate in raising young (Box 1), provide a testing ground for inclusive fitness theory. Despite differences in social complexity, the evolution of cooperative breeding across species requires an explanation for the same problem: why help others in raising young? According to inclusive fitness theory, selection will favour genes for helping behaviour when Hamilton's rule, $r_nB > r_oC$, is satisfied (Hamilton, 1963). Here, C is the number of offspring the actor can raise on it's own and r_o is its relatedness to them (direct fitness). B is the number of offspring the actor helps the recipient to raise and r_n is the actor's average relatedness to these offspring (indirect fitness). Therefore helping will evolve when it is a better strategy for passing genes to the next generation compared with breeding independently (Figure 1a).

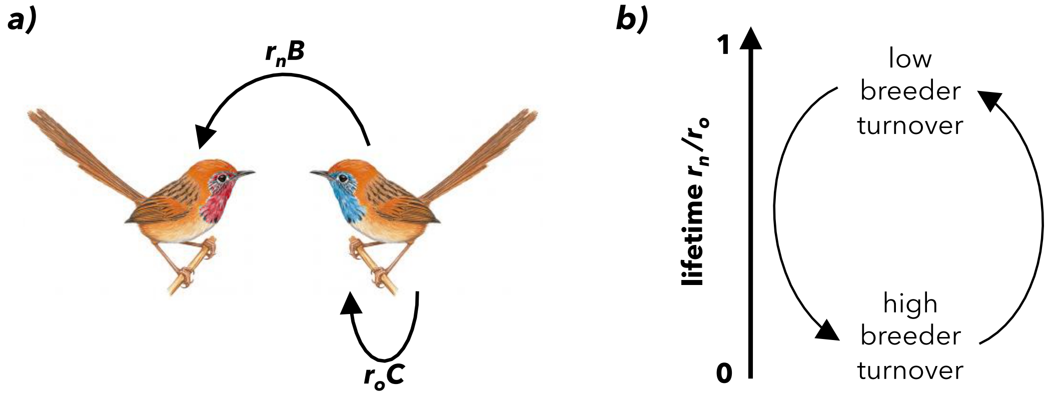


Figure 1. *a*) Helping behaviour is favoured over independent reproduction when the indirect fitness gains from helping (r_nB) are greater than the direct fitness gains from breeding (r_oC). *b*) Sterile helpers are predicted to evolve when relatedness to own offspring (r_o) is equal to relatedness to helped offspring (r_n) for life (lifetime r_n / r_o = 1). This requires low breeder turnover to ensure that helpers have full siblings to raise for their entire lifespans.

Recent empirical work has shown that monogamy provides a unifying explanation for the evolution of cooperative breeding in family groups across taxa. The logic is that older siblings can do as well by helping to raise full siblings as they can by breeding independently (on average $r_n = r_o = 0.5$). If the breeding female is polyandrous however, r_n falls below 0.5 and therefore selection will favour independent reproduction over helping (Boomsma, 2007; 2009). It follows that cooperative breeding should be more likely to evolve in monogamous than in polyandrous family groups, all else being equal. This prediction has received empirical support – cooperative breeding in birds, mammals and social insects is more likely to evolve from monogamous than from polyandrous ancestors (Hughes *et al.*, 2008; Cornwallis *et al.*, 2010; Duffy & Macdonald, 2010; Hechinger *et al.*, 2011; Lukas & Clutton-Brock, 2012a). Analogously, transitions to obligate multicellularity from single-celled organisms have only occurred in taxa where groups are formed clonally (Fisher *et al.*, 2013), which also satisfies the condition that $r_n = r_o$.

Outstanding Problems

Hamilton's rule is not just about relatedness. Life history and demographic factors will also influence the direct and indirect fitness benefits of cooperating by affecting the costs and benefits of helping as well as the kinship structure of social groups. For example, in family groups, the opportunity to inherit a breeding position is likely to be an important incentive for the evolution of cooperative breeding (Pen & Weissing, 2000; Cant & Field, 2001). Mortality rates and longevity may therefore influence the likelihood of transitions to cooperative breeding in some species. In addition, future breeding opportunities will influence whether helper sterility will evolve. Sterile worker castes are predicted to evolve when $r_n / r_o = 1$ for life so all that is required to satisfy Hamilton's rule is a small efficiency benefit to cooperating ($B > C$) (Boomsma, 2007; 2009). However, this condition is difficult to achieve due to breeder turnover (parents being likely to die before their offspring, Figure 1b) and requires the reversal of typical life history trade-offs (Heinze & Schrempf, 2008; Parker, 2010; Negroni *et al.*, 2016). Dispersal patterns are likely to shape investment in helping behaviour by influencing whether individuals breed in natal or non-natal groups which in turn influences within-group relatedness (Hamilton & May, 1977; Queller, 1992; Frank, 2001). Furthermore, cooperative breeding in non-family groups precludes indirect fitness as a sufficient explanation for the evolution of helping behaviour, further emphasising that factors other than relatedness can make helping the best strategy for passing on genes to future generations.

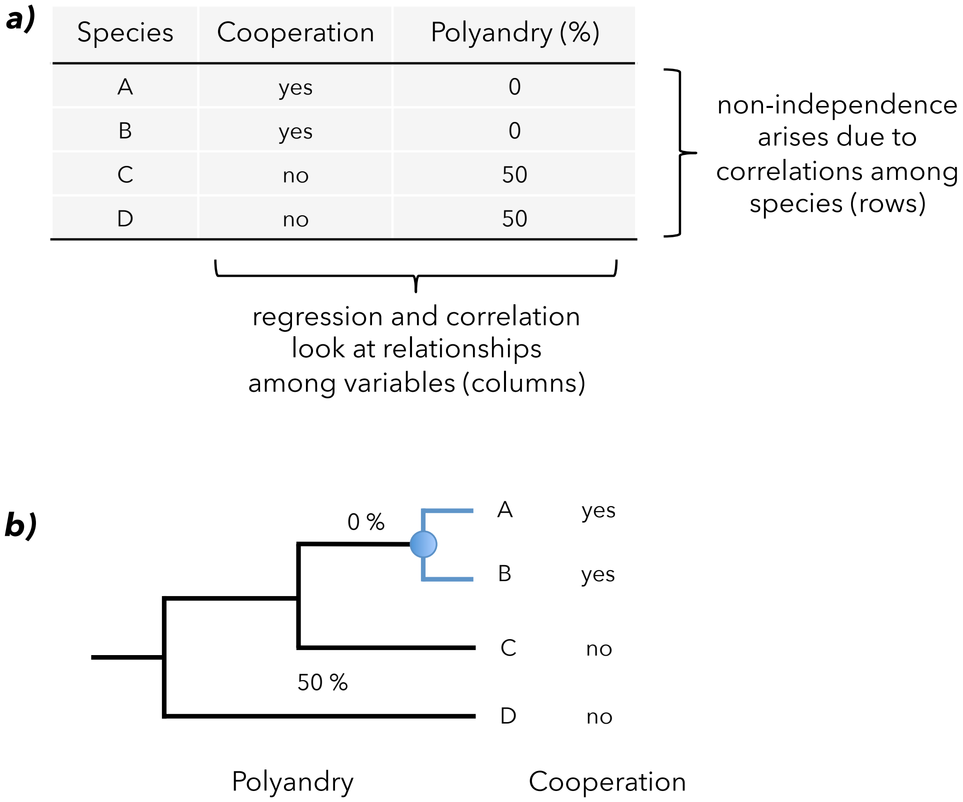
The Comparative Method Allows us to Test Hypotheses about the Evolution of Cooperative Breeding

Species vary in sociality, in life history traits and in demographic factors. We can use this variation to test hypotheses about the life history and demographic parameters that influence the evolution of cooperative breeding. The comparative method (Harvey & Pagel, 1991; Garamszegi, 2014) allows us to do this and has already been used to good effect in the study of social evolution (Bourke, 2014). Indeed, support for the prediction that high relatedness in family groups favours the transition to cooperative breeding has come from comparative studies. Specifically, transitions to cooperative breeding in birds and mammals occur from ancestral species where relatedness in family groups is high and eusociality has only evolved from monogamous ancestors in bees, wasps and ants (Hughes *et al.*, 2008; Cornwallis *et al.*, 2010; Lukas & Clutton-Brock, 2012a). However, the comparative method has rarely been used to explore the role of life history and demographic parameters in the evolution of cooperative breeding.

Birds as Data Points

Birds are a remarkably well studied group (del Hoyo *et al.*, 1992; Bennett & Owens, 2002; Cockburn, 2006) and therefore are a useful system for exploring how life history and demographic parameters shape the evolution of cooperative breeding. For many species we know how cooperatively breeding groups form and therefore whether these groups consist of family or of non-family members (Riehl, 2013). We know how much helpers and breeders in these species invest in various cooperative behaviours such as feeding young and territory defence (Cockburn, 1998; Hatchwell, 2009; Green *et al.*, 2016). Furthermore, rates of polyandry, annual survival, dispersal and maximum longevity have been measured in both cooperative and non-cooperative species and the geographic ranges of nearly all bird species have been mapped, allowing us to determine the types of habitat that they live in (Griffith *et al.*, 2002; Bennett & Owens, 2002; Jetz *et al.*, 2012; Healy *et al.*, 2014). We can use these variables to test hypotheses about the factors that favour the evolution of cooperative breeding.

Birds are also extremely useful as a model system because there is a published sample of 10 000 bird phylogenies, each of which is dated and includes all 9993 extant species (Jetz *et al.*, 2012) . This sample of phylogenies allows us to do three things (Garamszegi, 2014). First, having a phylogeny allows us to control for non-independence between species due to shared ancestry (Figure 2a). Second, by repeating any statistical models on multiple independently derived phylogenies we can take phylogenetic uncertainty into account. Although the evolutionary relationships between birds at the family and generic levels are relatively well resolved, relationships between species are poorly known in some clades (Jarvis *et al.*, 2014; Prum *et al.*, 2015). Third, because phylogenies document the evolutionary processes that give rise to extant species, we can use them in combination with data on extant species and statistical models of evolution to infer what the ancestors of living species looked like. This allows us to test hypotheses about the factors which favour the evolution of cooperative breeding (Figure 2b).



Species	Cooperation	Polyandry (%)
A	yes	0
B	yes	0
C	no	50
D	no	50

Figure 2. *a*) Species cannot be treated as independent data points because they share evolutionary history. Regression and correlation analyses must take this into account to avoid violating the assumption of independence between observations. *b*) A hypothetical phylogeny onto which ancestral state reconstructions of polyandry and cooperation from the table above have been mapped. In this example, low levels of female polyandry precede the origin of cooperation (blue dot).

Recent advances in phylogenetic comparative methods make it possible to incorporate this information into a single statistical model which can be used to explore the evolution of non-Gaussian traits, the evolution of multiple traits simultaneously and to conduct meta-analyses (a quantitative method for combining the results of different studies on the same topic) in a phylogenetic framework (Hadfield & Nakagawa, 2010; Garamszegi, 2014). This provides a powerful tool for testing evolutionary hypotheses about the evolution of cooperative breeding that would not have been feasible just a few years ago.

Thesis and Chapter Aims

In this thesis I use comparative analyses of cooperative breeding behaviour in birds to develop our understanding of the role of life history and demographic parameters in the evolution of cooperative breeding.

In chapter 2 I review evidence showing that long life makes the evolution of cooperative breeding in family groups more likely. I suggest that longevity in addition to monogamy has played a key role in the transformation of cooperatively breeding societies with helpers capable of reproducing into societies with sterile worker castes. Specifically, a complete overlap of generations is necessary to ensure that helpers can invest in raising full siblings for their entire lives.

In chapter 3 I test between alternative hypotheses for why cooperatively breeding birds are longer lived than non-cooperative species. Long life has been argued to be a consequence of cooperative breeding: group living reduces mortality due to predation. It has also been argued that long life is a cause of cooperative breeding: inheriting a breeding position leads to enhanced reproductive success. Using ancestral state reconstructions I show that the ancestors of cooperatively breeding species are longer-lived than the ancestors of non-cooperative species, supporting the hypothesis that enhanced reproductive success once a territory is inherited favours the evolution of cooperative breeding.

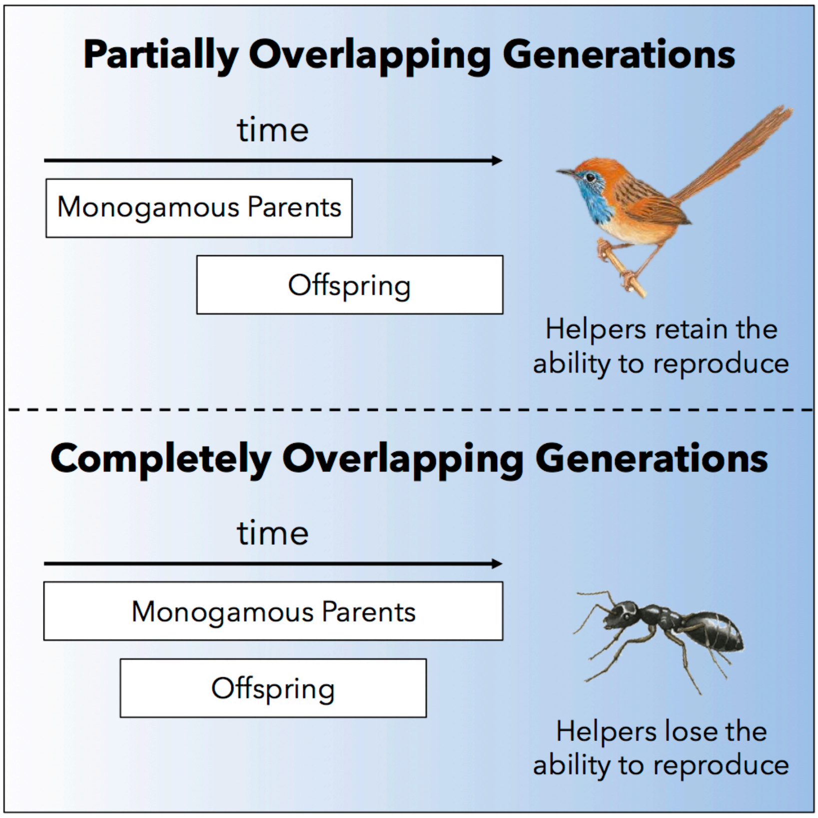
In chapter 4 I use the difference in the amount of help that female and male helpers provide at their natal nest to infer a role for direct fitness in shaping investment in helping behaviour. Since helpers of each sex are equally related to the young in their natal group, the difference in the amount that they help is likely to result from differences in strategies to maximise future reproductive success. Consistent with this prediction, I find that the sex that has a higher probability of breeding in its natal group invests more in helping behaviour.

In chapter 5 I explore transitions to cooperative breeding in non-family and family groups. It has been argued that these are variants of the same breeding strategy, linked through a dependency on group living and therefore that monogamy fails to provide a general explanation for the evolution of cooperative breeding. Using ancestral state reconstructions I demonstrate that transitions to cooperative breeding in non-family and family groups result from distinct evolutionary trajectories and that cooperative breeding in non-family groups evolves from relatively polyandrous ancestors while cooperative breeding in family groups evolves from relatively monogamous ancestors.

In the final chapter I test whether the reproductive costs of care explain variation in how much breeders adjust their parental behaviour when they have helpers at the nest. Breeders are expected to reduce their investment in parental care when the costs of caring are high and to maintain their investment when the costs of caring are low. I used adult survival as a proxy for the costs of care and a statistical effect size to estimate how breeders adjust their effort in parental care when they have helpers at the nest. I found a positive relationship between these variables: breeders reduced their investment when survival was low (and the costs of care high) and maintained their investment when survival was high (and the costs of care low). This supports the prediction that breeders adjust their investment in offspring in response to the reproductive costs of care.

Chapter 2

How to Make a Sterile Helper



ABSTRACT

The sterile worker castes found in the colonies of social insects are often cited as archetypal examples of altruism in nature. The challenge is to explain why losing the ability to mate has evolved as a superior strategy for transmitting genes into future generations. We propose that two conditions are necessary for the evolution of sterility: completely overlapping generations and monogamy. A review of the literature indicates that when these two conditions are met we consistently observe the evolution of sterile helpers. We explain the theory and evidence behind these ideas, and discuss the importance of ecology in predicting whether sterility will evolve using examples from social birds, mammals and insects. In doing so, we offer an explanation for the extraordinary lifespans of some cooperative species which hint at ways in which we can unlock the secrets of long life.

INTRODUCTION

Altruistic behaviour is epitomised by the sterile worker castes found in the colonies of social insects. Instead of attempting to reproduce, workers invest in a variety of cooperative behaviours ranging from brood care and colony defence to forming bivouacs and tending fungus gardens (Wilson, 1971). In extreme cases, workers have become morphologically specialised to perform these tasks. For example, the heads of worker turtle ants, *Cephalotes varians*, are disc shaped, allowing them to act as living doors to their nests (Powell, 2008) while the swollen crops of large honeypot ant workers, *Myrmecocystus mexicanus*, permit them to act as storage vessels of sugar, water and lipids (Rissing, 1984). These behaviours have an obvious benefit to the colony as a whole but pose important questions about the process of natural selection (Darwin, 1859; Dawkins, 1976): how can a gene for altruism spread when those carrying it are sterile?

Inclusive fitness theory, first proposed by W. D. Hamilton in the 1960s (Hamilton, 1964a; b), provides a solution to this problem. Altruistic individuals are able to transmit their genes to future generations indirectly by improving the reproductive success of relatives that carry the same gene. Family groups provide ideal conditions for the evolution of altruism, simply because family members are more likely to share genes, relative to the population as a whole. Relatedness in family groups can however still vary due to differences in the number of breeders contributing to the family gene pool. This led to the prediction that life-time monogamy is necessary for the evolution of sterility since it ensures that helpers can pass on as many genes by raising full siblings as they can by having their own young (Boomsma, 2007; 2009; 2013). However, not all monogamous cooperative species have sterile helpers. Most notably, monogamy drives the evolution of cooperative breeding in vertebrates (Cornwallis *et al.*, 2010; Lukas & Clutton-Brock, 2012a), an entire lineage in which all helpers are able to reproduce (Stacey & Koenig, 1990; Jennions & Macdonald, 1994). Why have sterile helpers evolved in some monogamous species but not in others?

Here, we argue that longevity plays a key role in determining which monogamous species evolve sterile helpers. To do so, we break down the evolution of sterility into two steps. The first step is the formation of a cooperatively breeding group in which helpers are not sterile but retain the ability to breed later in life. Being long-lived makes this more likely to happen. The second step is the transformation of a cooperatively breeding group where all individuals are fertile to one with sterile helpers. For this to happen, helpers need to be able to invest in raising full siblings for the duration of their lives. This is possible if breeders live longer than their offspring that help. We then discuss what stops cooperative groups with fertile helpers from transforming into species with sterile helpers – this depends on the interplay between ecology and longevity. These arguments make sense of the remarkable lifespans of some cooperative species. For example, they help to explain why harvester ant queens, *Pogonomyrmex owyheei*, can live for up to thirty years (Keller, 1998) and why naked mole-rats, *Heterocephalus glaber*, have become a model organism for studying the mechanisms of ageing, including cancer resistance (Buffenstein, 2005; 2008; Liang *et al.*, 2010).

STEP 1: FORM A COOPERATIVELY BREEDING GROUP

The first step in the evolution of a sterile helper is the formation of a cooperatively breeding group (Bourke, 2011; West *et al.*, 2015). Here, we define a cooperatively breeding group as a family in which offspring delay dispersal and help their parents in raising their siblings. The evolution of cooperative breeding is predicted to be more likely to happen from monogamous than from polyandrous non-cooperative ancestors (Boomsma, 2007; 2009; 2013). This is because monogamy ensures a favourable exchange rate when helpers are weighing up if they can pass on more genes by helping or by breeding (Box 1). Evidence from birds and mammals supports this prediction: cooperatively breeding species are more likely to evolve from monogamous than from polyandrous ancestors (Cornwallis *et al.*, 2010; Lukas & Clutton-Brock, 2012a).

BOX 1. The Relatedness Exchange Rate

When should one individual (the actor) give up it's own reproduction and help to raise someone else's (the recipient) young? Inclusive fitness theory predicts that altruistic helping of this kind will evolve when Hamilton's rule, $r_nB > r_oC$, is satisfied (Hamilton, 1963; Queller & Strassmann, 1998; Gardner *et al.*, 2011). That is, when the number of offspring the actor helps the recipient to produce (B), to whom the actor is related by r_n, is greater than the number of offspring the actor could produce if it didn't help (C), to whom it is related by r_o. The ratio of these relatedness coefficients effectively gives the actor an exchange rate which it can use to value the recipient's offspring against it's own (Grafen, 1991). Clearly, cooperation is most easily favoured when the relatedness exchange rate (r_n / r_o) equals one, meaning that as long as there is some small efficiency benefit to cooperating ($B > C$) the actor can pass on more genes by helping than by breeding independently. In sexually reproducing species the relatedness exchange rate equals one when offspring delay dispersal and help their parents in raising full siblings. On average, helpers are as related to their full siblings as they are to their own offspring. Hence the prediction that the evolution of sterile helpers will happen in family groups in which the breeding female has mated monogamously (Boomsma, 2007; 2009). For sterility to evolve however, the relatedness exchange rate needs to equal one for the duration of the actor's lifetime. This is only possible if helpers can invest in raising full siblings for the duration of their lifespans.

Cooperative Breeding Birds Are Long-Lived

In addition to being less polyandrous than non-cooperative species, cooperatively breeding birds are also long-lived. The cooperatively breeding red-winged fairy-wren, *Malurus elegans*, which weighs little more than a ballpoint pen, can live for up to sixteen years (Russell & Rowley, 2000), whereas the similarly sized non-cooperative Zebra finch, *Taeniopygia guttata*, only lives up to five years (Zann & Runciman, 1994) (Figure 1*a*, *b*). Similarly, pairs of cooperatively breeding Seychelles warblers, *Acrocephalus sechellensis*, may remain together nine years (Richardson *et al.*, 2007; Hammers *et al.*, 2015) while non-cooperative bearded tits, *Panurus biarmicus*, live for two to three years on average (Wilson & Peach, 2006) (Figure 1*c*, *d*). This trend has been confirmed across bird species: cooperative breeders are longer-lived on average than non-cooperative species, after accounting for confounding factors such as latitude and body mass which also influence longevity (Arnold & Owens, 1998; Beauchamp, 2014; Downing *et al.*, 2015).

Why do we see this association between cooperative breeding and longevity? There are two possible reasons. Firstly, longevity may be a consequence of cooperative breeding. Living in a group has been suggested to protect group members from external causes of mortality, through increased predator vigilance for example, which in turn selects for longer life (Williams, 1957; Wasser & Sherman, 2010). Alternatively longevity may be a cause of cooperative breeding. Theoretical models of the evolution of cooperative breeding find that long-lived species are more likely to make the transition to cooperative breeding than short-lived species because long life enhances reproductive success once a nest is inherited (Pen & Weissing, 2000; Wild & Koykka, 2014).

Whether long-life is a cause or a consequence of cooperative breeding has been tested in birds (Downing *et al.*, 2015). If a long life makes cooperative breeding more likely to evolve, then we would expect the ancestors of cooperative breeders to be longer lived than the ancestors of non-cooperative species. If long-life is a consequence of the benefits of group living then longevity should increase after cooperative breeding has evolved.

Figure 1. Cooperatively breeding birds are relatively long-lived. The cooperatively breeding red-winged fairy-wren, *Malurus elegans* (*a*), is longer-lived than the similarly sized but non-cooperative zebra finch, *Taeniopygia guttata* (*b*). Similarly, the cooperatively breeding Seychelles warbler, *Acrocephalus sechellensis* (*c*), is longer-lived than the similarly sized but non-cooperative bearded tit, *Panurus biarmicus* (*c*). Images from Wikipedia Commons (*a* to *d*): Cas Liber, Jim Bendon, Christian Hauzar, and Martin Mecnarowski.

Ancestral state reconstructions have demonstrated that the ancestors of cooperative breeders had higher rates of annual survival (a proxy for longevity) than the ancestors of non-cooperative breeders, and there were no changes in annual survival after a species became cooperative (Downing *et al.*, 2015). These results confirm the prediction that long-life makes the evolution of cooperative breeding more likely. This supports the idea that the opportunity to reproduce via nest inheritance plays a important role in the evolution of cooperative breeding, as predicted by theoretical models of the evolution of cooperative breeding (Pen & Weissing, 2000; Wild & Koykka, 2014). It also appears that exceptionally long-lived cooperatively breeding birds, such as the red-winged fairy-wren, *M. elegans*, are more polyandrous than non-cooperative species with similar lifespans. This suggests that when relatedness between helpers and offspring is low – hence reducing the opportunity for indirect fitness benefits – living a long time is important for obtaining a breeding position to secure direct fitness benefits.

Patterns Of Longevity In Cooperative Mammals

There is mixed evidence regarding whether cooperatively breeding mammals are long-lived. Among small ground-dwelling mammals (those weighing less than 60 kg), maximum lifespans are higher in cooperatively breeding species than in non-cooperative species (Williams & Shattuck, 2015). In contrast, across all mammals, there appears to be no difference in the annual survival rates of cooperatively breeding and non-cooperatively breeding species (Lukas & Clutton-Brock, 2012b). In fact, the pattern is in the opposite direction to that predicted: non-cooperative breeders have higher rates of annual survival than cooperative breeders, although this difference is not statistically significant. It is currently unclear why large size should make a difference to the relationship between cooperative breeding and longevity.

Nest Inheritance Is Associated With Cooperative Breeding In Invertebrates

All of the evidence discussed so far concerning the role of longevity and the evolution of cooperative breeding has come from vertebrates. Is the evolution of cooperative breeding in family groups in other clades also associated with longevity? Evidence suggests it is. The ancestral termite is likely to have been a long-lived cooperatively breeding cockroach (Bignell *et al.*, 2010). This conclusion is based on comparisons between extant termites and the cockroach genus *Cryptocercus*, which form a monophyletic group. *Cryptocercus* are wood-feeding cockroaches that provide bi-parental care in family groups (Bell *et al.*, 2007). They live in chambers and burrows chewed into the logs they feed on. This provides a relatively safe nesting environment which means they are relatively long-lived: their life-cycle takes 8 years to complete from hatch to hatch. As in birds, nest inheritance resulting in the opportunity to reproduce is thought to have been an important incentive for philopatry and the evolution of cooperation in prototermites (Thorne *et al.*, 2003; Johns *et al.*, 2009; Bignell *et al.*, 2010; Hoffmann & Korb, 2011).

The opportunity for nest inheritance is not restricted to long-lived species. For example, the paper wasp, *Polistes dominulus*, has an annual life-cycle and relatively high mortality rates (Shreeves *et al.*, 2003). In this species, newly founded social groups typically consist of sisters but from 15% to 35% of females are unrelated (Queller *et al.*, 2000; Monnin *et al.*, 2009; Leadbeater *et al.*, 2010). Nest-inheritance compensates for the low relatedness exchange rate and makes cooperation worthwhile: females that inherit the dominant position produce more offspring than do solitary females (Leadbeater *et al.*, 2011). Furthermore, cooperative breeding ensures that young are raised to independence even if their parent dies, a mechanism known as assured fitness returns (Gadagkar, 1990; Field *et al.*, 2000). Remarkably, subordinate females that are next in line to inherit the dominant position invest less in care than subordinate females that are unlikely to inherit a breeding position, further reflecting how cooperative behaviour is shaped by future direct fitness (Cant & Field, 2001). This example emphasizes that it is the opportunity to reproduce via nest inheritance that provides an incentive for cooperative breeding, and this occurs in both long-lived and short-lived species.

STEP 2: TRANSFORM YOUR COOPERATIVE GROUP

Once a cooperative breeding group has formed the second step in the evolution of a sterile helper is selection for reduced reproductive function in helpers (Bourke, 2011; West *et al.*, 2015). For this to happen, a helper needs to be able to re-invest its potential reproductive effort into raising full siblings for its entire lifespan rather than for just a fraction of it (Boomsma, 2007; 2009). When this is the case, the relatedness exchange rate equals one and drops out of Hamilton's rule (Box 1) and all that is required for sterility to evolve is a small efficiency benefit to helping ($B > C$). From this argument, it follows that two conditions are necessary for the evolution of a sterile helper. First, strict lifetime monogamy of the breeding female is required to ensure that helpers are investing in the production of full siblings (Boomsma, 2007; 2009). This appears to be the case: monogamy is the ancestral condition for all examined origins of eusociality in bees, wasps and ants (Hughes *et al.*, 2008). Second, a complete overlap of generations is required to ensure that a helper is able to invest in raising full siblings for the duration of its lifetime.

The extent of generational overlap influences the lifetime relatedness exchange rate. Consider the three following examples. In the first, parents have short lifespans and die before their young reach reproductive maturity resulting in non-overlapping generations (Figure 2*a*). At best, members of the same cooperative group will be full siblings and the relatedness exchange rate will equal one half. This appears to characterise some cooperatively breeding species. For example in co-foundress associations of the paper wasp, *P. dominulus*, and in breeding groups of long-tailed tits, *Aegithalos caudatus*, group members are often siblings (Queller *et al.*, 2000; Russell & Hatchwell, 2001; Hatchwell & Woodburn, 2003; Monnin *et al.*, 2009; Leadbeater *et al.*, 2010). As expected from Hamilton's rule, in these species the benefits of cooperating are high and the costs are low which compensates for helping to raise the offspring of siblings (Leadbeater *et al.*, 2011; Hatchwell *et al.*, 2014). In the second example there is a degree of generational overlap between parents and offspring (Figure 2*b*). Here, offspring can raise full siblings for some of their lifespans, but not all. While their parents are alive offspring often delay reproduction to help, but once their parents die, independent reproduction becomes a better fitness maximising strategy than helping. This stops lifetime commitment to a sterile role. As seen earlier, a degree of overlap between reproductive generations appears to typify the life histories of most cooperatively breeding vertebrates and some social insects. In the third example parents live longer than their offspring resulting in completely overlapping generations (Figure 2*c*). Consequently, helpers can invest in raising full siblings for the duration of their lives. The indirect fitness gains from helping are therefore always as profitable as the direct fitness gains from breeding independently, eliminating conflict over reproduction and permitting the evolution of sterile helpers.

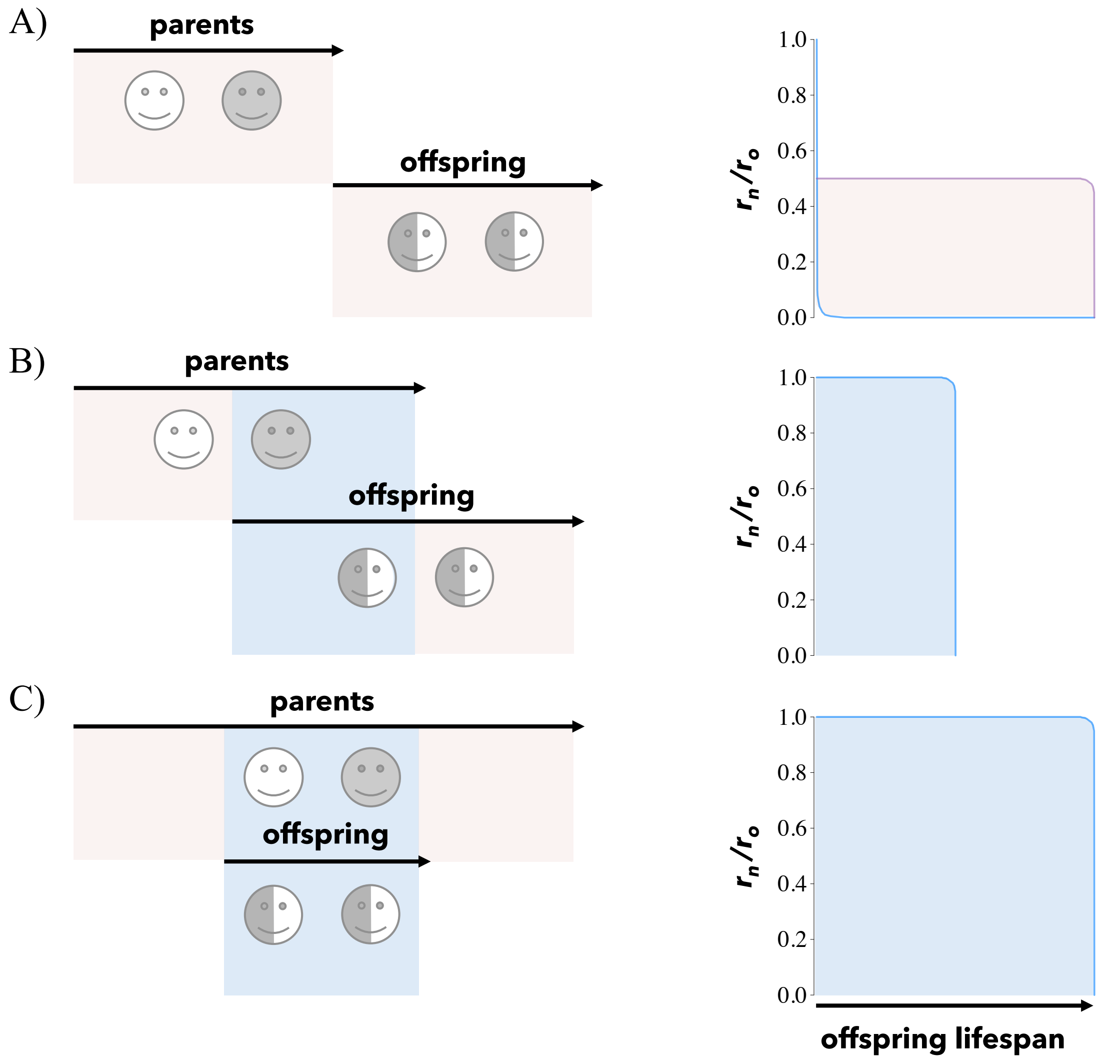


Figure 2. Generational overlap affects the lifetime relatedness exchange rate. (*a*) When there is no overlap between parents and offspring, social groups will consist of siblings. In this case, the relatedness exchange rate (r_n / r_o) is equal to a half (pink shaded region). (*b*) When there is some generational overlap, offspring can do as well by helping to raise full siblings as they can by breeding independently while their parents are alive (blue shaded region). (*c*) When there is complete generational overlap and parents are longer-lived than their offspring, offspring can invest in raising full siblings for the duration of their lifespans, favouring lifetime commitment to a non-reproductive role. This can be achieved in different ways: through divergent selection on the lifespans of breeders and helpers or through the co-option of a bivoltine life-cycle (which always refers to an annual life cycle).

What matters for the evolution of sterility is that helpers can invest in raising full siblings for the duration of their lifespans. Most commonly, this will happen when breeders are relatively longer-lived than helpers: whether helpers live for a few days or for several years, they will have a life-long supply of full siblings to raise if their parents live longer than they do. It is possible, however, that helpers can invest in raising full siblings for their entire lifespans with minimal overlap between parent and offspring generations. For example, if the queen dies once her last eggs are laid, as long as older helpers can invest in raising this brood for their entire lives, selection can favour sterility. This requires that older helpers only live for the period of dependency of the last brood. If older helpers were alive when this last brood reaches independence, it would be better for them to retain the ability to reproduce and raise their own young.

The Rate of Extrinsic Mortality Influences Lifespan Evolution

An obvious question that arises is how do breeders become longer lived than helpers? Evolutionary theories of the evolution of ageing predict that a key factor shaping an organism's lifespan is the rate of extrinsic mortality that occurs, for example, due to predation or disease (Williams, 1957; Hamilton, 1966; Abrams, 1993). When extrinsic mortality is low, selection favours long-term investment in survival whereas when extrinsic mortality is high, investment in early reproduction is favoured over investment in survival. Recent support for this prediction comes from a study on how the ability to fly has shaped the evolution of mammal and bird lifespans (Healy *et al.*, 2014). Flight is assumed to reduce the rate of extrinsic mortality by allowing species to escape predation and unfavourable conditions. Across 1368 species of birds and mammals the study found that species capable of flight have longer lifespans than similar-sized species that are not capable of flight. Theory and evidence therefore suggest that the rate of extrinsic mortality can shape lifespan evolution.

BOX 2. One Genome, Different Lifespans

What are the proximate mechanisms underlying differences in longevity between individuals with the same genome? In the honey bee, *Apis mellifera*, being fed royal jelly determines which females become queens. Queens have an average lifespan of between one and two years while helpers have an average lifespan of six to eight weeks (Free & Spencer-Booth, 1959; Page & Peng, 2001; Remolina *et al.*, 2007; Remolina & Hughes, 2008). Mating itself also seems to contribute to longer life. In Ansell's mole rat, *Fukomys anselli*, sexual activity appears to enhance the lifespans of breeders which live about twice as long as non-breeders despite being equivalent in intrinsic quality (Dammann & Burda, 2006; Dammann *et al.*, 2011). Similarly, in the ant, *Cardiocondyla obscurior*, queens mated to either a fertile or a sterilised male lived significantly longer than virgin queens (Schrempf *et al.*, 2005). In this species, the expression of a putative aging gene, *NLaz*, is related to queen longevity, and the changes in gene expression with age are in the opposite direction to those seen in the common fruit fly, *Drosophila melanogaster* (Wyschetzki *et al.*, 2015). *Juvenile Hormone* may also play a key role in regulating differences in longevity between breeders and helpers. *Lasius niger* ant queens that were experimentally treated with *Juvenile Hormone* laid fewer eggs, had increased activity rates, reduced maternal care and had higher mortality when exposed to a fungal pathogen compared to a control group with un-manipulated levels of *Juvenile Hormone* (Pamminger *et al.*, 2016).

Division of Labour Leads to Differences in the Lifespans of Breeders and Helpers

A reproductive division of labour is vital to the evolution of lifespan differences between breeders and helpers. This is because it gives the unusual condition that individuals within the same social group may experience very different rates of extrinsic mortality. For example, if helpers protect breeders from predation they would experience elevated rates of extrinsic mortality while the breeders would experience reduced rates. Evidence suggests that individuals in different roles within social groups do indeed experience different rates of extrinsic mortality which leads to differences in longevity. In the weaver ant, *Oecophylla smaragdina*, and in the leaf-cutting ant *Acromyrmex subterraneus brunneus*, large helpers perform riskier tasks than smaller helpers and in line with the prediction that the rate of extrinsic mortality shapes investment in lifespan, small helpers live longer than large helpers (Chapuisat & Keller, 2002; Camargo *et al.*, 2007). Similarly, breeder and helper naked mole-rats, *H. glaber*, both live for over 25 years in captivity where they are protected from extrinsic mortality but in the wild, helpers live for four years on average while breeders live for over 17 years (Sherman & Jarvis, 2002; Buffenstein, 2008). The proximate factors underlying differences in the lifespans of individuals with the same genome (Box 2) provide a unique opportunity for developing our understanding of the ageing process.

Insect Life-Cycles And Lifespans

Solitary insect species with bivoltine life-cycles have two broods per year as an adaptation to seasonality (bivoltine life-cycles always refers to an annual life cycle). The first brood is produced early in the year and develops fully while the second brood is produced later in the year and enters diapause until the cycle begins anew the following year. Inherent in a bivoltine life-cycle is the ability to produce a short-lived helper caste early in the season which helps to rear a relatively long-lived breeding caste later in the year, which then overwinters. The co-option of a bivoltine life-cycle has been argued to explain why first brood females in *Polistes* wasps help to rear second broods (Hunt & Amdam, 2005). Since helpers from the first brood are typically raising full siblings for their entire lifespans (they die at the end of the breeding season), the condition that the relatedness exchange rate is equal to one for the duration of the helper's lifespan is satisfied. Similar processes are thought to explain lifespan differences in other lineages including the bumble bee, *Bombus terrestris* (Amsalem *et al.*, 2015; Séguret *et al.*, 2016). These life-cycles further emphasise the point that it is complete generational overlap, rather than life span per se that is key for the evolution of sterility. While the two are usually correlated, in bivoltine species, a shorter lifespan does not reduce the probability of overlap.

Breeders Are Longer-Lived Than Helpers in Some Cooperative Species

An important consequence of a reproductive division of labour and bivoltinism is that breeders can evolve to be longer-lived than helpers. This gives us our second necessary condition for the evolution of sterility – a complete overlap of generations. Are breeders longer-lived than helpers? This appears to be the case in some cooperative species. For example, there are considerable differences in the lifespans of breeders and helpers in many species of ants, wasps and bees, and the magnitude of the difference in lifespans appears to be positively associated with colony size (Kramer & Schaible, 2013). Furthermore, the queens of ant and termite colonies are extremely long-lived, with average lifespans of 10 and 11.5 years respectively (Keller

& Genoud, 1997; Keller, 1998). This is particularly striking given that the average lifespan of non-cooperative insect species is 0.1 years (Keller & Genoud, 1997).

Although differences in the lifespans of breeders and helpers exist in some cooperative species, the extent to which these differences are associated with sterility has not been quantitatively explored. As Figure 3 demonstrates, in some species with large differences in longevity between breeders and helpers, helpers are completely sterile, lacking functional ovaries. In other species however helpers are capable of reproducing despite expecting to live less than half as long as breeders. For example, there appears to be an asymmetry in the lifespans of breeders and helpers in naked mole-rats, *H. glaber* (Buffenstein, 2008). In this species less than one percent of females within a colony ever get to breed and physical aggression by the breeding female appears to suppress sexual maturation. Individuals less than eight months old are capable of reproducing however, should the opportunity arise (Buffenstein, 2005). Similarly, queens in the slave-making ant, *Harpagoxenus sublaevis*, inhibit ovarian development in their helpers who can otherwise produce sons (Franks *et al.*, 1990). In the Japanese ant, *Diacamma rugosum*, which lacks a morphologically differentiated queen caste, the dominant female mutilates the thoracic appendages of other females to stop them from mating, although some do reproduce (Figure 3) (Tsuji *et al.*, 1996; Baratte *et al.*, 2006). In haplodiploid species such as ants, the ability of female helpers to produce sons without mating appears to limit the evolution of complete sterility and the loss of ovaries among helpers appears to be rare (Bourke, 1988; Ratnieks *et al.*, 2006; Dijkstra & Boomsma, 2006; Kronauer *et al.*, 2010; Alpedrinha *et al.*, 2013). These patterns suggest that an asymmetry in the lifespans of helpers and breeders does not guarantee the evolution of complete sterility. Our argument however is that without completely overlapping generations lifetime commitment to a non-reproductive role cannot be favoured by selection. Although not all species with an asymmetry in the lifespans of helpers and breeders will have evolved sterility, species with sterile helpers will have completely overlapping generations, at least ancestrally.

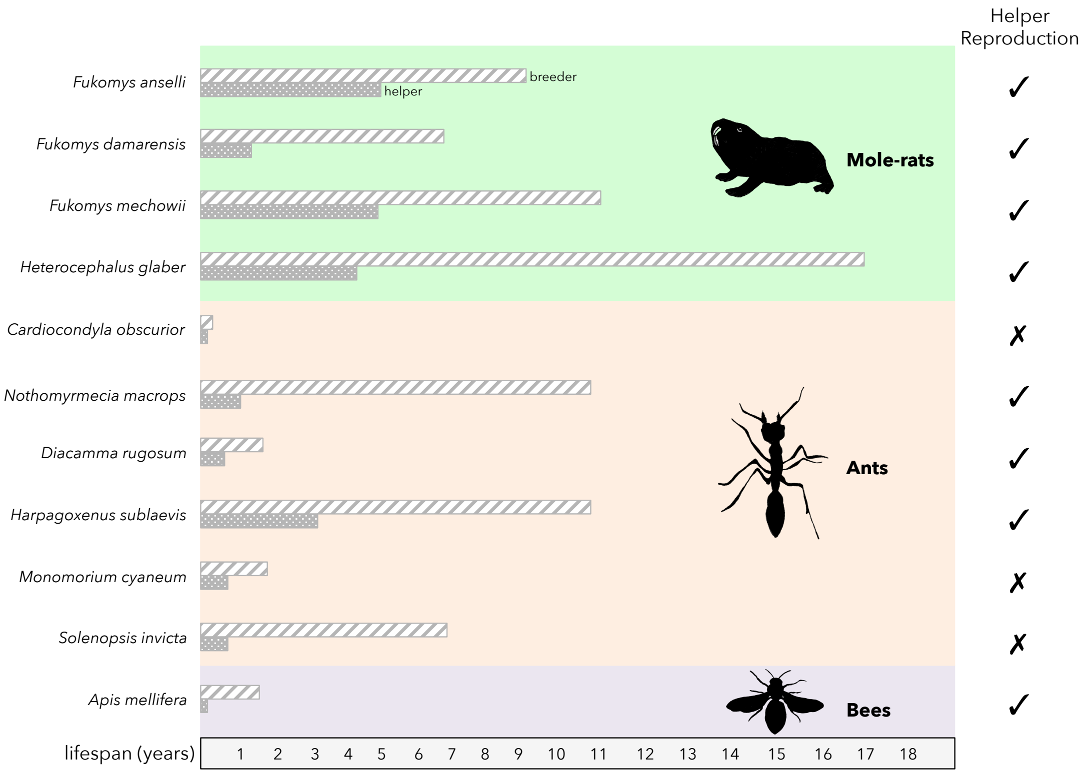


Figure 3. The difference in the average lifespans of female breeders (hatched bars) and female helpers (dotted bars) varies across social species. Despite considerable differences in the lifespans of breeders and helpers in some species, helpers are still able to reproduce. Data are from a mixture of field and laboratory populations. Sources: *Fukomys anselli* (Dammann & Burda, 2006), *Fukomys damarensis* (Schmidt *et al.*, 2013), *Fukomys mechowii* (Dammann *et al.*, 2011), *Heterocephalus glaber* (Buffenstein, 2008), *Cardiocondyla obscurior* (Schrempf *et al.*, 2005), *Nothomyrmecia macrops* (Sanetra & Crozier, 2002), *Diacamma rugosum* (Tsuji *et al.*, 1996), *Harpagoxenus sublaevis* (Bourke *et al.*, 1988), *Monomorium cyaneum*, *Solenopsis invicta* (Tschinkel, 1987), *Apis mellifera* (Winston, 1987).

Other factors may have also played a role in the evolution of complete worker sterility. For example, there may be physical constraints on the ability of very small workers to maintain their ovaries and as the size of the colony increases, the chance of any one worker reproducing becomes negligible, hence diminishing the strength of selection for investment in reproduction (Bourke, 1999; Bourke, 2011). Selection may also favour the retention of ovaries among workers. For example, female workers produce sons following queen loss in some haplodiploid species (such as ants, bees and wasps) where workers also regularly produce trophic eggs. Indeed, although workers are usually committed to a life-long non-reproductive role in haplodiploids, the loss of ovaries among workers appears to be rare (Bourke, 1988; Ratnieks *et al.*, 2006; Dijkstra & Boomsma, 2006; Kronauer *et al.*, 2010; Alpedrinha *et al.*, 2013). Determining how these factors influence the evolution of sterility and how they interact with longevity remains to be addressed.

PROTECT THE QUEEN

Although low levels of female polyandry favour the evolution of cooperative breeding in vertebrates, a complete overlap of generations, which is required for the evolution of sterile helpers, is absent from most species (Koenig & Dickinson, 2004; 2016). This is surprising given that there is a clear reproductive division of labour in many cooperatively breeding species (Stacey & Koenig, 1990; Jennions & Macdonald, 1994; Koenig & Dickinson, 2016) which, as argued above, sets the scene for helpers and breeders to experience different rates of extrinsic mortality, eventually resulting in completely overlapping generations. The question this raises is why breeders and helpers in most cooperative vertebrates do not experience different rates of extrinsic mortality despite a reproductive division of labour?

Ecology is likely to play an important role. In the social insects, two ecological syndromes are associated with the evolution of sterility: fortress defence and life insurance (Queller & Strassmann, 1998). Fortress defenders feed and live in a protected site and include some termites, social aphids, social shrimps, social thrips and ambrosia beetles. Life insurers feed outside the nest and include ants, bees and wasps. In both fortress defenders and life insurers, the nest is a valuable, defensible resource (Bourke, 2011). Crucially, this nest protects the queen from predation while helpers may be exposed to predation when foraging or defending the nest for example. In contrast, among most cooperatively breeding vertebrates, the nesting site does not predictably guarantee that breeders and helpers experience different rates of extrinsic mortality as it does in fortress defenders and life insurers. For example, in one of the most socially advanced birds, the obligately cooperative white-winged chough, *Cyanocorax melanorhamphos*, breeders and helpers perform all of the same tasks ranging from building the nest to guarding the young (Heinsohn, 1992; Heinsohn & Cockburn, 1994). This difference in ecology means that in most cooperatively breeding vertebrates all individuals within the social group are exposed to similar rates of extrinsic mortality independently of whether they are a helper or a breeder. The only exception to this generality are the mole-rats. Mole-rats live and feed in a network of subterranean burrows as do fortress defenders (Jarvis, 1981). As seen, differences in the lifespans of breeders and helpers suggest that they exposed to different levels of extrinsic mortality in the wild (Sherman & Jarvis, 2002; Buffenstein, 2008).

How to quantify differences in the ecology of cooperatively breeding species with and without sterile helpers is an empirical challenge. Although the distinction between fortress defenders and life insurers is useful and it has been argued that vertebrates show a combination of these two syndromes (Korb & Heinze, 2008), what seems essential is the extent to which the queen is protected from predation relative to workers.

Post-Reproductive Sterility Can Evolve In Multi-generational Families

Another interesting difference between the social insects and some social vertebrates is the existence of multi-generational families in the latter. In our own species for example, parents, their offspring and their grand-offspring may all live within the same family group (Hawkes *et al.*, 1997; 1998; Sear & Mace, 2008). In social insects however this appears to be rare. Group members within ant and termite colonies are typically parents and their offspring (Wilson, 1971; Hughes *et al.*, 2008). This makes group kin-structure more predictable in social insects than it is in social vertebrates living in multi-generational families, which undergo age-related changes in relatedness. For example, grandmothers are less related to their daughter's offspring than their own while daughters are equally related to their mother's offspring as their own.

From a theoretical perspective these sorts of asymmetries in relatedness that arise with age can lead to conflict over reproduction within social groups and ultimately drive the evolution of post-reproductive lifespans (Johnstone & Cant, 2010; Croft *et al.*, 2015). Support for this prediction comes from a study on the evolution of menopause in the killer whale, *Orcinus orca* (Brent *et al.*, 2015). In killer whales, male and female offspring are both philopatric and mating occurs between groups meaning that female's become more closely related to group members as they age, favouring investment in helping late in life. There is also evidence from our own species to suggest that age related changes in relatedness may favour the evolution of post-reproductive lifespans. In societies with female biased dispersal, immigrant females are only related to their own offspring in their adopted groups while older females are related to other group members, including the immigrant females' offspring. This favours younger females in reproductive competition with older females who are still able to gain indirect fitness benefits by helping late in life (Lahdenperä *et al.*, 2012; Mace & Alvergne, 2012).

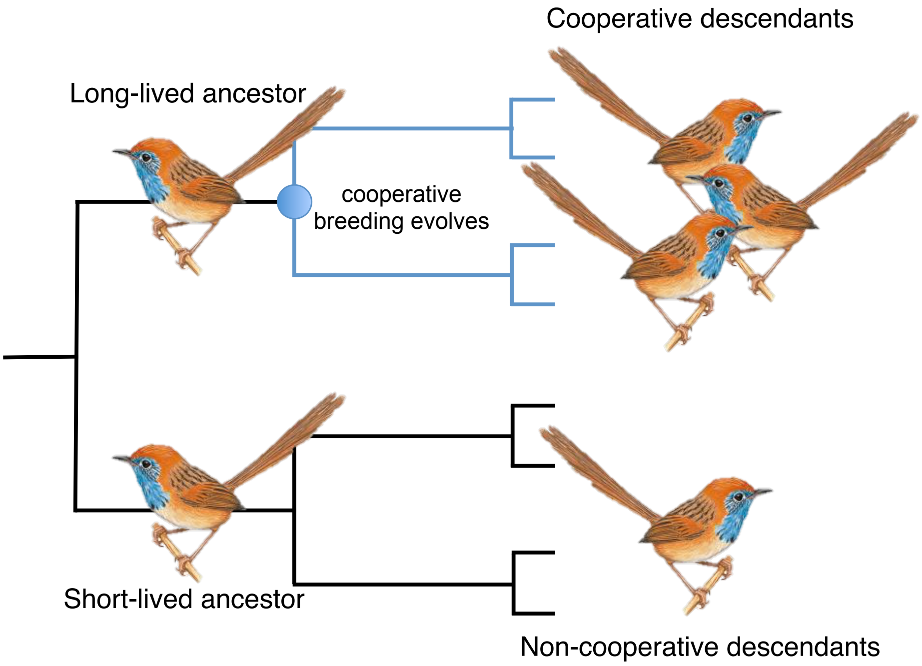
PREDICTIONS AND CONCLUSIONS

We have shown that making a sterile helper requires the evolution of cooperative breeding followed by selection for reduced reproductive function in helpers. This requires two conditions to be satisfied: the group's breeding female should be monogamous and there should be a complete overlap of generations. These conditions ensure that helpers can do as well by helping as they could do by breeding for the duration of their lives, eliminating conflict over reproduction. The second condition is satisfied when breeders and helpers are exposed to low and high rates of extrinsic mortality respectively or through the co-option of a bivoltine life-cycle. Further empirical observations on individual species and comparative analyses across species should be used to confirm that there is complete generational overlap in species with sterile helpers. Ancestral state reconstructions of worker and breeder lifespans can then be used to explore their co-evolution. We expect that differences in breeder and worker lifespans should be greatest in the ancestors of species with sterile helpers. One difficulty in testing this hypotheses is that once sterile helpers have evolved, the colony becomes the unit of selection meaning that complete overlap of generations may be lost (Helantera, 2016).

Overall, cooperative behaviour accounts for the exceptional thirty year lifespans of harvester ant queens, *P. owyheei* and for cancer resistance in naked mole-rats. Since the same genome can produce vastly different lifespans, social species provide an ideal system for studying the epigenetics of senescence and other proximate mechanisms underlying the ageing process. This could help us unlock the secrets to designing extraordinary lifespans.

Chapter 3

Sex, Long Life and the Evolutionary Transition to Cooperative Breeding in Birds



ABSTRACT

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 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.

INTRODUCTION

Individuals help raise young produced by others in approximately one tenth of all bird species (Cockburn, 2006; Jetz & Rubenstein, 2011). 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 (Stacey & Koenig, 1990; Koenig & Dickinson, 2004). For example, while many passerines breed in their first year of adulthood (Bennett & Owens, 2002), 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 (Cockburn *et al.*, 2008). Social queues of this kind reach their extreme in white-winged choughs, *Corcorax melanorhamphos*, in which individuals delay breeding until they are at least four years of age, during which time they help to build the nest, incubate and feed the young and participate in group defence (Rowley, 1978).

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 (Wiley & Rabenold, 1984; Brown, 1987). Pen and Weissing's (2000) 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 to verbal models (Arnold & Owens, 1998; Hatchwell & Komdeur, 2000) this relationship results regardless of any ecological constraints on reproduction such as slow territory turn over. 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 (Zack & Ligon, 1985; Arnold & Owens, 1998; Beauchamp, 2014). 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 itself selects for longer life (Williams, 1957; Wasser & Sherman, 2010). 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 (Pen & Weissing, 2000; Wild & Koykka, 2014), 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 (Boomsma, 2007; 2009). 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 (Cornwallis *et al.*, 2010) and mammals (Lukas & Clutton-Brock, 2012a) (see also Hughes et al.'s analysis of the affect of monogamy on transitions to eusociality in the social insects (Hughes *et al.*, 2008)) . 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: 1) that helpers queue for reproductive positions and during this time they have limited access to direct reproduction, 2) that cooperative breeders are indeed longer lived than non-cooperative breeders, 3) that long life preceded the evolution of cooperative breeding rather than evolving as a result of group living, and 4) 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.

METHODS

Data Collection

In Pen & Weissing's model (2000), 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 (Burke *et al.*, 1989; Faaborg *et al.*, 1995; Riehl, 2011) are excluded from our definition of cooperation.

We obtained data on whether cooperative breeders queue for breeding positions via key word searches including the terms '*Species name AND demography OR reproduction*' using Web of Science and Google Scholar up to and including 10th 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 average ages at which individuals first bred for 39 species of bird (cooperative $N_{\text{species}} = 19$, non-cooperative $N_{\text{species}} = 20$) (supplementary Table 1). This is the most complete sample we could obtain for cooperative breeders whilst the sample of non-cooperative breeders was chosen to give a balanced design and these species 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. (2010) and updated this list to include recently published data on extra-pair paternity up to and including 10th March 2015. We collected data on three potential measures of life span: annual survival, average survival and maximum longevity. These were found through key word searches using the terms '*Species name AND survival OR longevity*' using Web of Science and Google Scholar up to and including 10th March 2015. We also carried out forward and backward citation searches on major reviews (Karr *et al.*, 1990; Yom-Tov *et al.*, 1992; Siriwardena *et al.*, 1998; Peach *et al.*, 2001; Beauchamp, 2014). Our different measures of survival were highly correlated (supplementary Figures 1*a*, *b* and *c*). We used annual survival in our analyses since 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 (Beauchamp, 2014). In total we compiled survival and promiscuity estimates for 238 species of bird (cooperative $N_{\text{species}} = 35$, non-cooperative $N_{\text{species}} = 203$) (supplementary Table 2).

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 (Arnold & Owens, 2002), body mass (Lindstedt & Calder, 1981; Karr *et al.*, 1990; Promislow, 1993; Healy *et al.*, 2014) and latitude (Karr *et al.*, 1990; Møller, 2007). We collected data on body mass (grams) from the *Handbook of the Birds of the World* (del Hoyo *et al.*, 1992) 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 (Harvey & Pagel, 1991) we adopted a comparative approach analysing data using Bayesian phylogenetic linear mixed models (BPMMs) (Lynch, 1991; Hadfield & Nakagawa, 2010; Hadfield, 2010b). BPMMs take a phylogenetic tree and convert it into a variance-covariance matrix that represents all pair wise ‘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_{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 (Jetz *et al.*, 2012). 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.

Analyses

We performed four sets of analyses using BPMMs conducted in MCMCglmm (Hadfield *et al.*, 2014) in R version 3.0.2 (R Core Team, 2013). 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 (2 level factor: cooperative vs. 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 (2 level factor:

cooperative vs. 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 (Schielzeth & Forstmeier, 2009). We then investigated whether helpers gain a significant amount of direct fitness whilst 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_{species} = 40, note that 5 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 (2 level factor: cooperative vs. 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 complimentary 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 x 2 variance-covariance matrix for the interaction between trait and phylogeny and calculated the correlation as $COV_{survival,\ cooperative} / sqrt(VAR_{survival} * VAR_{cooperative})$. We also fitted a 2 x 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 of cooperative (1) versus non-cooperative (0)) 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 (4-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 BayesTraits' (Pagel & Meade, 2006) 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. Since BayesTraits 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 (2 level factor: cooperative vs. 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 2x2 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 (Warnes & Burrows, 2013) in R which combines Raftery and Lewis' run length diagnostic with Gelman and Rubin's convergence diagnostic (Raftery & Lewis, 1992). Estimates of parameters were calculated as the mode of posterior samples and their significance was assessed by examining the credible interval: if the 95% credible intervals 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 supplementary information.

RESULTS

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 (β) = 1.38, 95% credible interval (CI) = 0.83 to 1.83; N_{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 1a,b). While queuing to become breeders, helpers had little access to direct reproduction, siring less than 8 % of young on average (Figure 1c) (proportion of young sired by dominant breeders: $\beta = 0.98$, CI = 0.91 to 0.99; $N_{\text{species}} = 40$).

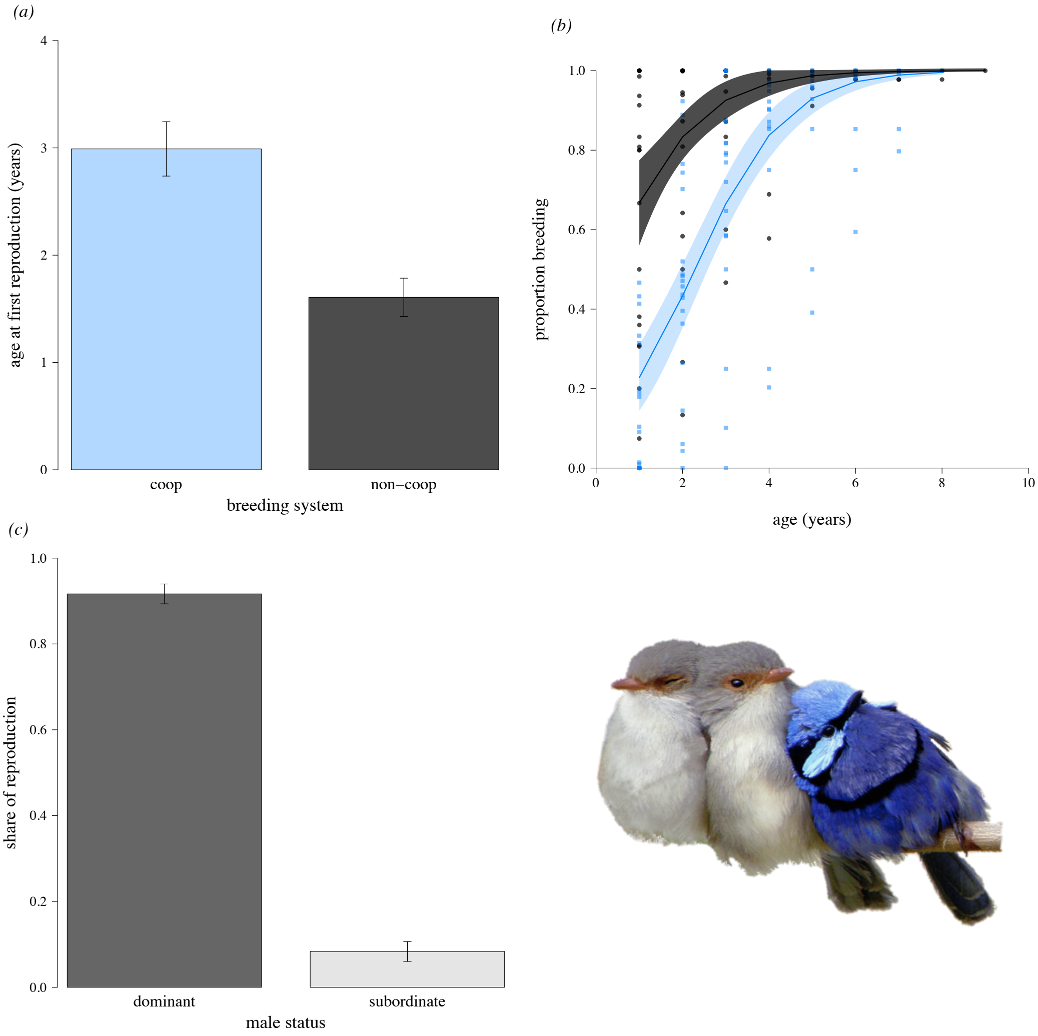


Figure 1. (*a*), Mean age at first reproduction is later in cooperative breeders than in non-cooperative breeders. Data show mean ± standard error ($N_{\text{species}} = 39$). (*b*), Fewer cooperative breeders (blue / grey, squares) breed in a given age class compared with non-cooperative breeders (black,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

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 to 0.68; $N_{\text{species}} = 238$) (Figure 2).

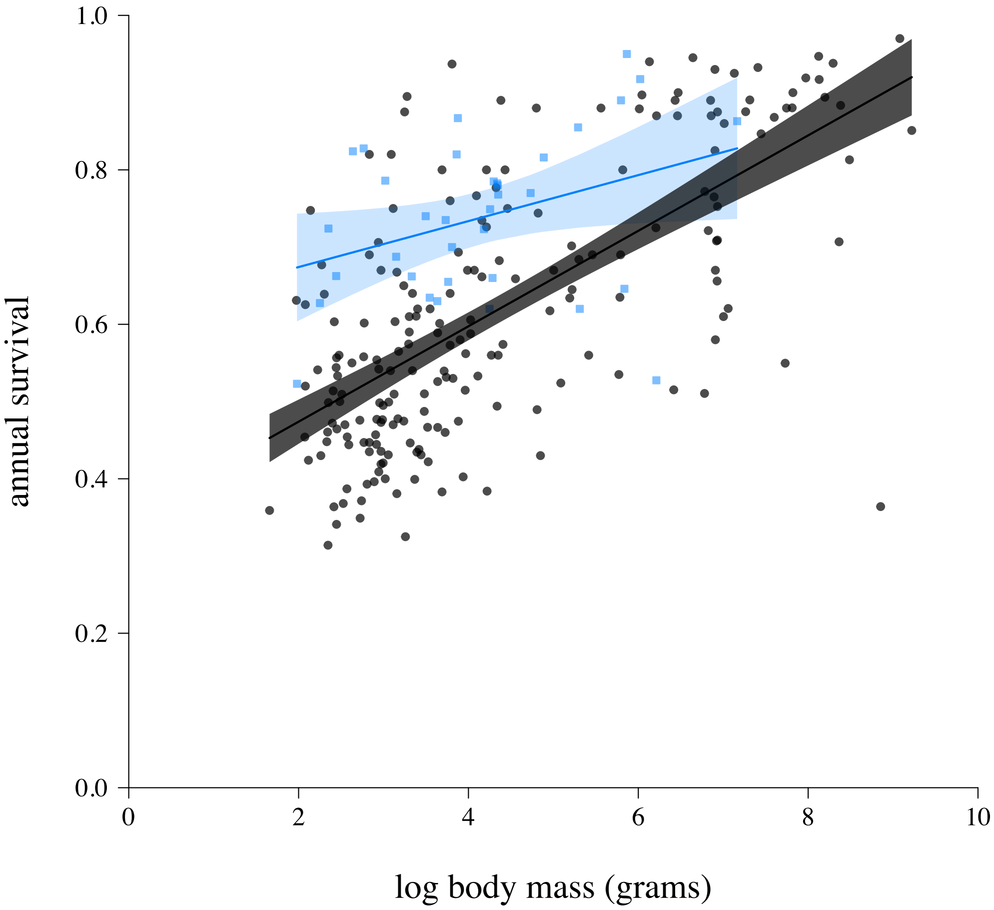


Figure 2. Cooperative breeders (blue / grey, squares) have higher levels of survival than non-cooperative breeders (black, circles). Regression lines are presented with 95% credible intervals (N_{species} = 238). Excluding the wild turkey, *Meleagris gallopavo*, the outlier in the bottom right corner,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

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 to 0.71; N_{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: β = 0.32, CI = 0.01 to 0.72 ; N_{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: β = -0.28, CI = -0.76 to 0.26; N_{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 (Pagel & Meade, 2006)). 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 cooperation (Bayes Factor = 0.41, weak evidence of a difference) (supplementary Figure 2). Taken together, these results show that transitions to cooperative breeding are more likely if a species is long lived.

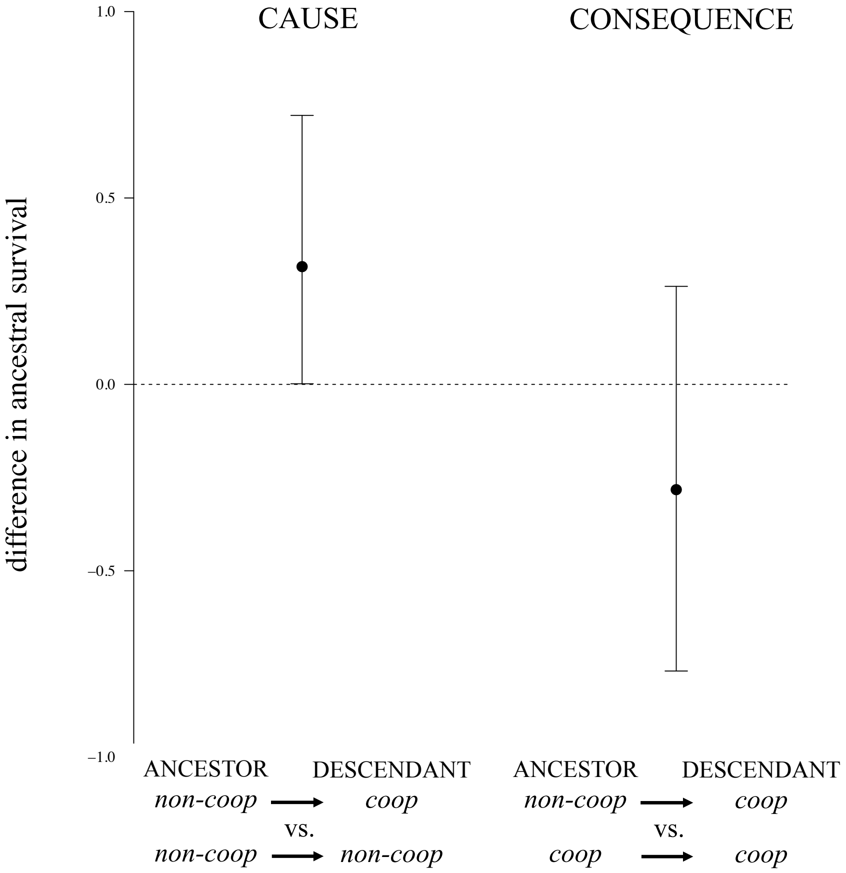


Figure 3. There was a significant difference in survival between non-cooperative ancestors of cooperative descendants and non-cooperative ancestors of non-cooperative descendants: the 95% credible interval of the estimate does not include zero. In contrast, survival did not differ between non-cooperative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

Is long life more pronounced in promiscuous cooperative breeders?

There was a positive relationship between promiscuity and survival in cooperative breeders whilst this relationship was negative in non-cooperative breeders (difference in slopes: $\beta = 1.33$, CI = 0.14 to 2.37; $N_{\mathrm{species}} = 238$) (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.

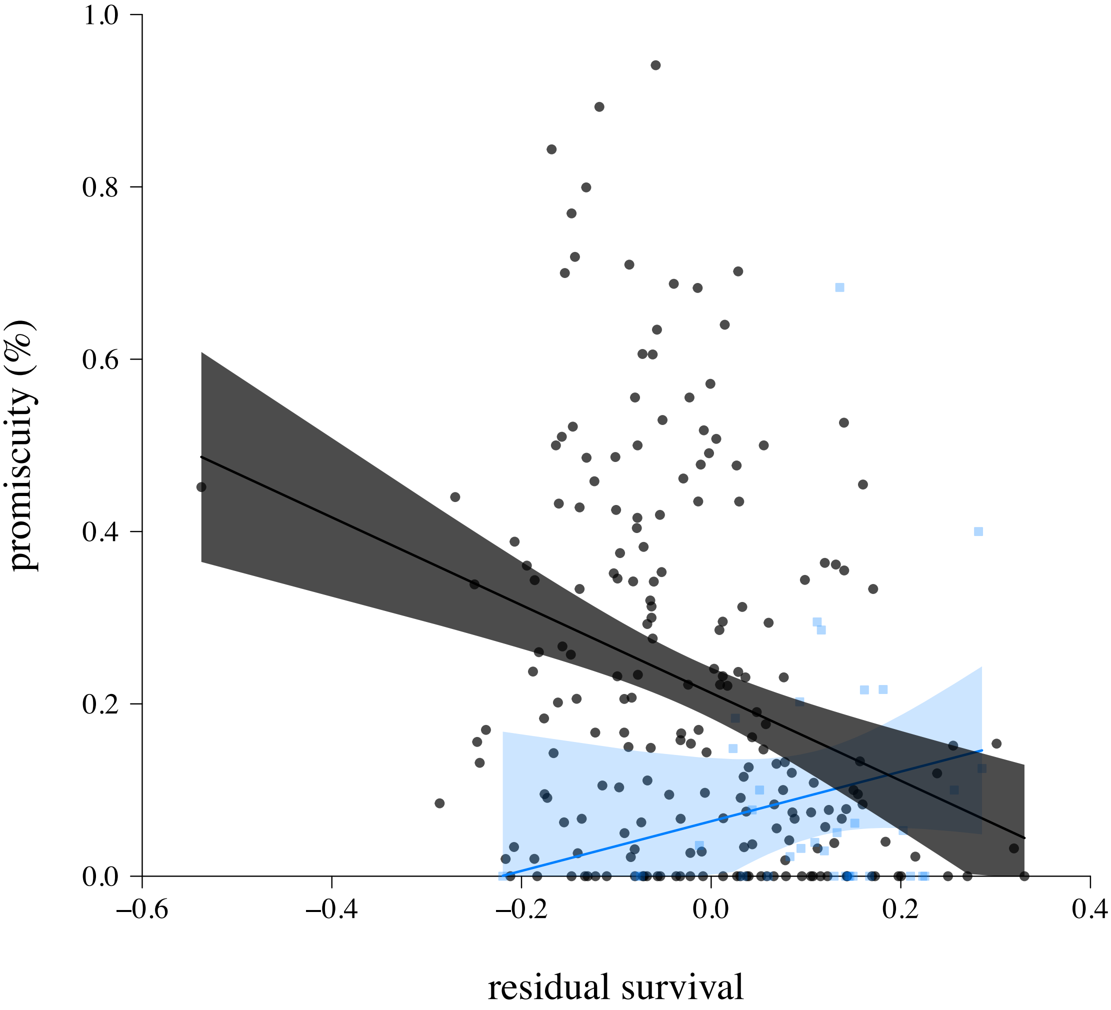


Figure 4. As promiscuity increases among non-cooperative breeders (black, circles) survival decreases whilst in cooperative breeders (blue / grey, squares) there is an increase in survival as promiscuity increases. Regression lines are presented with 95% credible intervals (N_{species} = 238). Excluding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

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 nest mates. 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 (Zack & Ligon, 1985; Arnold & Owens, 1998; Beauchamp, 2014), 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 (Williams & Shattuck, 2015; Healy, 2015).

Recent theoretical and empirical work has emphasised monogamy as an important predictor of transitions to cooperative societies (Boomsma, 2007; Hughes *et al.*, 2008; Boomsma, 2009; Cornwallis *et al.*, 2010; Lukas & Clutton-Brock, 2012a) yet there are numerous species that do not fit this pattern. The Australian magpie, *Gymnorhina tibicien*, and the superb fairywren, *Malurus cyaneus*, are well known examples of promiscuous cooperative species (Mulder *et al.*, 1994; Hughes *et al.*, 2003). 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 comprised of breeders and subordinate helpers, very much like those of cooperatively breeding birds (Queller & Strassmann, 1998; Queller *et al.*, 2000; Field *et al.*, 2006). Low levels of relatedness between individuals in these species make direct reproduction the best fitness maximising strategy. Similarly 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 (Leadbeater *et al.*, 2011). 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.

Chapter 4

Sex Differences In Helping In Cooperative Societies Are Explained By Future Direct Fitness Benefits

ABSTRACT

Cooperatively breeding birds have provided useful model systems for demonstrating the action of kin selection in the evolution of helping behaviour. While it is recognised that direct fitness benefits are also important, these are more difficult to detect, being realised years into the future if a helper inherits a breeding position. In this study, we investigate differences in helping behaviour between male and female helpers before dispersal to detect evidence of direct fitness effects on helping behaviour. Crucially, male and female helpers at the natal nest are equally related to offspring in their care, so any differences in investment are likely to result from differences in strategies to maximise future direct reproductive success. We used comparative analyses of helping behaviour across 26 species of cooperatively breeding bird to test how potential differences in future reproductive success caused by variation in philopatry and female promiscuity shape helping behaviour. We found that females helped more than males when they were the philopatric sex and when rates of female promiscuity were high. We go on to show that constraints on independent reproduction determine which sex is philopatric. These results confirm that direct fitness benefits shape the evolution of helping behaviour.

INTRODUCTION

Social groups in cooperatively breeding species are characterised by a reproductive division of labour – some individuals breed and others help to raise offspring (Wilson, 1971; Stacey & Koenig, 1990; Jennions & Macdonald, 1994). How much helpers invest in care has been shown to depend on the level of relatedness to offspring, suggesting that helping may be favoured by kin selection as a strategy to increase indirect fitness (Griffin & West, 2003; Cornwallis *et al.*, 2009; Green *et al.*, 2016). However, there is also a striking difference across cooperative species in the levels of investment between male and female helpers (Cockburn, 1998; Stiver *et al.*, 2005; Lloyd *et al.*, 2009; Zahed *et al.*, 2010; Ross *et al.*, 2013). Since female and male helpers are equally related to the offspring in their natal group, this difference in investment is unlikely to be driven by kin selection. Exploring why one sex helps more than the other could, therefore, provide evidence for the role of direct fitness benefits in the evolution of cooperative breeding (Heinsohn & Legge, 1999; Cant & Field, 2001; 2005).

Future breeding opportunities within the group may have differential effects on the direct fitness of helpers, depending on their sex. Specifically, philopatry is predicted to favour investment in helping at the natal nest when this increases the reproductive success of helpers when they become breeders in the future (Kokko *et al.*, 2001; Clutton-Brock *et al.*, 2002). This may occur if survival is correlated with group size or if current offspring produced go on to become helpers in the future (Stacey & Koenig, 1990; Heinsohn, 1992; Creel & Creel, 2015). Several within-species studies have reported a positive relationship between philopatry and investment in helping (Komdeur, 1994; Dunn *et al.*, 1995; Langen, 1996; Clutton-Brock *et al.*, 2002; Woxvold *et al.*, 2006), but in general variation in the degree of philopatry is likely to be limited within species. Since either sex can be philopatric across species of cooperatively breeding birds (Stacey & Koenig, 1990; Koenig & Dickinson, 2016), between species variation provides an opportunity to test this prediction. Variation in female promiscuity has also been suggested to lead to differential effects on the future direct fitness of female and male helpers (Charnov, 1981). High rates of female promiscuity are predicted to favour male investment in helping due to paternity uncertainty: male helpers may be more related to their nest-mates than they are to the offspring produced by their future mate. In contrast, female helpers will be more related to their future offspring than to their natal nest-mates, favouring investment in direct fitness.

As well as determining sex differences in helping behaviour, selection to maximise future direct fitness may also determine which sex is philopatric and which sex disperses. When the tenure of breeding males exceeds the age at which females first reproduce and there are opportunities for independent reproduction it is predicted that females will disperse from their natal groups to reproduce with unrelated males (Clutton-Brock & Lukas, 2012). Under these circumstances, philopatry will be male biased. In contrast, when there are constraints on independent reproduction female philopatry will be favoured over male philopatry. For example, if it is only possible to raise young with the help of others, then the reproductive success of females will depend on being part of a group whereas male reproductive success is limited by access to mates and opportunities for extra-pair paternity (Emlen & Oring, 1977; Davies *et al.*, 1995a; Davies & Hartley, 1996).

In this study, we explore how selection to maximise future direct fitness shapes the evolution of helping behaviour by estimating the extent of sex differences in helping across 26 species of cooperatively breeding bird. We quantify the difference in how much female and male helpers invest in behaviours such as incubating and feeding their siblings using a statistical effect size. We then use a phylogenetic meta-analytic approach to test whether sex-biased philopatry and female promiscuity explain differences between the sexes in helping behaviour. Secondly, we ask whether sex-biases in philopatry are explained by constraints on independent reproduction, measured as the proportion of nests with helpers in each population. How these variables relate to each other is unknown. One possibility is that constraints on independent reproduction, by driving sex-biased philopatry, may also drive differences in how much the sexes help. Alternatively, constraints on independent reproduction may be negatively correlated with female promiscuity due to the cost of parental care, which may then favour increased female investment in helping. We examine support for these alternatives using phylogenetic path analyses.

METHODS

Data Collection

To measure the amount of help that males and females provide, we searched the published literature using Scopus and the Web of Knowledge for studies measuring helping effort in cooperatively breeding birds. We used the following topic search term: '*(feed* OR provision* OR help* OR defen*) AND species name*'. We searched both common and scientific species names including known synonyms. We started with the cooperative species listed by Riehl (2013) and updated this to include newly recognized cooperative breeders. We excluded cooperative breeders which do not show year round territoriality and philopatry of at least one sex and those in which helpers of the opposite sex disperse into the group. For well-studied species for which no relevant studies could be found using Scopus and the Web of Knowledge, we contacted individual researchers to request data. We followed the Preferred Reporting Items for Systematic Reviews and Meta-Analysis statement for extracting effect sizes (Liberati *et al.*, 2009; Moher *et al.*, 2009).

Effect Sizes

We calculated effect sizes as the standardized mean difference, *Hedges' d* (Nakagawa & Cuthill, 2007; Nakagawa *et al.*, 2014). Full details and equations for how this was calculated along with its sampling variance are given in the supplementary R script. In our case this was most commonly the difference in the number of feeding trips made per hour by the average male and female helper. By estimating the difference in the average contributions made by male and female helpers, our effect size is independent of the number of helpers of each sex. Positive values indicate that males help more, negative values that females help more and a value of zero indicates no difference in helping effort between the sexes. Our final sample size included 97 effect sizes from 34 studies representing 26 cooperatively breeding bird species (supplementary Figure 1; supplementary Table 1).

Publication Bias Tests

We explored how our effect sizes are influenced by sample size in two ways. Firstly, we tested whether there is a relationship between effect size and sample size using Egger's regression method (Egger *et al.*, 1997; Moreno *et al.*, 2009). The precision with which main effects are estimated depends on sample size. Therefore we expect scatter when sample size are small and increasing precision as sample sizes increase. This gives rise to a 'funnel' shaped plot. If there is no relationship between effect size and sample size, we would expect a regression slope of zero. We regressed the mean difference in helper effort against the inverse standard error of the effect sizes in the MCMCglmm R package (Hadfield, 2010a; R Core Team, 2013). We included species, study and phylogeny as random effects and weighted each effect size by the square of its sampling variance. We found no relationship between the mean difference in helper effort and the inverse of the standard error (slope: $\beta = 0.03$, CI = -0.1 to 0.2, $N_{species} = 26$, $N_{effect\ sizes} = 97$; supplementary Figure 2). Second we conducted a trim and fill analysis in the 'metafor' R package (Viechtbauer, 2010) which estimated that our sample would require three extra effect sizes to generate a symmetric funnel plot. Because this approach does not correct for non-independence between effect sizes we conclude from these publication bias tests that our calculated effect sizes are not biased by sample size.

Demographic Data

We collected data on the level of female promiscuity, the direction of sex bias in philopatry and constraints on independent reproduction from the literature for the 26 species for which we obtained effect sizes (supplementary Table 2). We measured promiscuity as the proportion of broods in a population with at least one extra-pair chick. This is a commonly reported metric and provides a population level measure of female promiscuity and is related to the indirect fitness benefits available to group members – higher levels of extra-pair paternity reduces relatedness within family groups and the potential indirect fitness benefits available from helping. In total, we found promiscuity data for 20 of the 26 species.

We categorised each species as having either a male bias in philopatry or a female bias in philopatry based on longitudinal data. For most of the species in our data set, sex-specific dispersal rates have not been estimated and although individuals of either sex may disperse at various ages, treating philopatry as a binary trait captures the tendency for one sex to be more likely to breed in its natal group than the other. In four species, both sexes are philopatric ('equal' in supplementary Table 2). Due to the rarity of female biased systems in our data set, we treated these species as being female biased in our analyses to increase statistical power. Given that the philopatry hypothesis predicts that the sex that has most to gain from its natal group will help more, if both sexes stand to gain equally then we would expect no difference in helping behaviour. By treating these species as female biased we are therefore less likely to detect an effect of philopatry, making our results conservative.

We used two surrogates to estimate constraints on independent reproduction: the proportion of nests with helpers and mean group size for each species. We assume that when all nests have helpers, individuals need to be part of a group in order to breed in the future and therefore potential constraints on independent reproduction are high. Similarly, we assume that larger group sizes reflect constraints on independent reproduction since more individuals are needed to raise young. The proportion of nests with helpers and group size are highly correlated ($r = 0.82$) therefore we only used the proportion of nests with helpers in our analyses to avoid increasing the error associated with our parameter estimates due to collinearity among fixed effects (Freckleton, 2011).

Analyses

Phylogenetic meta-analysis

We used Bayesian phylogenetic mixed models (BPMMs) implemented in the MCMCglmm R package (Hadfield, 2010a; R Core Team, 2013) for our analyses. These models allow the incorporation of several random effects that take into account non-independence between data points arising due to multiple effect sizes per study and per species as well as phylogenetic relationships and enable the amount of variation that they explain in the response variable to be quantified. In addition, we weighted each data point by the sampling error associated with each effect size to account for differences between studies in sample sizes. We assessed model convergence by assessing plots of chain mixing and levels autocorrelation. Parameter estimates are reported as the posterior mode (β) and credible interval (CI) of the posterior distribution of the Markov chain. Relationships were considered significantly different from 0 where the credible interval of the posterior mode did not include zero. Full details of burn-in, run length, priors as well as the model formula, including error structures, are reported in the supplementary R script.

We accounted for phylogenetic uncertainty in our BPMMs by marginalizing over the posterior distribution of bird trees published by Jetz *et al.* (2012). We did this by calculating the parameter estimates for the BPMM based on 1000 different phylogenetic covariance matrices included sequentially as random effects at successive iterations of the Markov chain in each model. Each time we updated the phylogenetic covariance matrix in the model, we used the values of the latent variables and variance components calculated using the last covariance matrix as starting values for the next tree in the sequence. For further details see the supplementary R script and the methods section of Ross *et al.* (2013).

Sex differences in helping

We estimated the overall difference in investment in helping between the sexes across species by constructing an intercept only model with the mean difference in helper effort between the sexes as the response variable (using a Gaussian error distribution). To test whether sex-biased philopatry and female promiscuity explain sex differences in helping behaviour, we constructed a BPMM with the mean difference in helper effort between the sexes (using a Gaussian error distribution) as the response variable and philopatry (2 levels: female bias or male bias) and the proportion of broods with extra-pair paternity (arcsine and z transformed) as our fixed effects. We then modeled the relationship between the mean difference in helper effort between the sexes and each of these fixed effects separately to ensure that our results were not influenced by inter-correlations between our explanatory variables.

Direction of sex-bias in philopatry

We tested whether constraints on independent reproduction measured as the proportion of nests with helpers, explains the direction of sex bias in philopatry using a BPMM with philopatry (female bias = 0, male bias = 1) as the response variable and the proportion of nests with helpers (arcsine and z transformed) as our fixed effect.

Phylogenetic path analysis

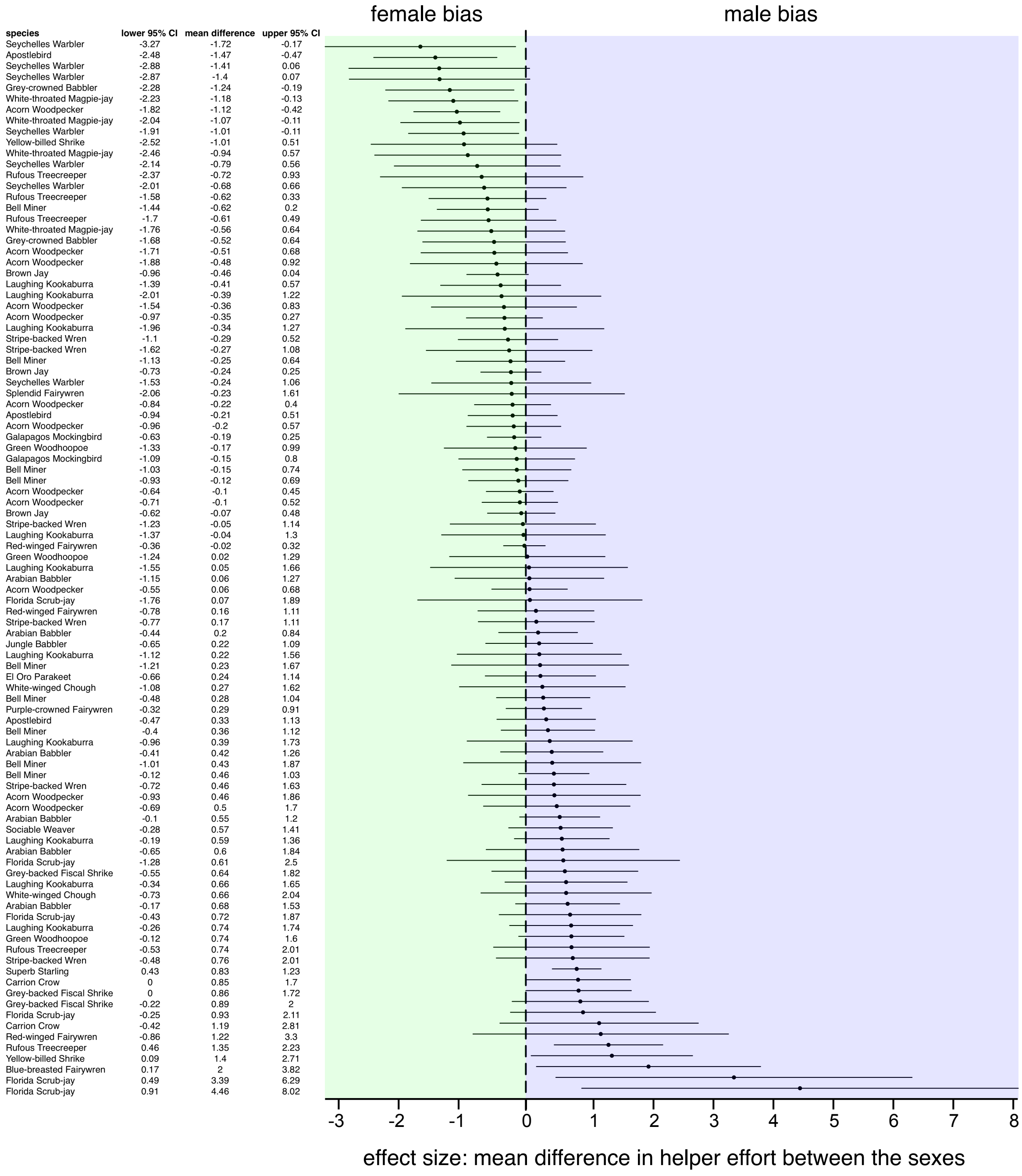
We used phylogenetic path analysis (Hardenberg & Gonzalez-Voyer, 2013) to explore the potential causality underlying the relationships between philopatry, constraints on independent reproduction, female promiscuity and the mean difference in helper effort between the sexes. We constructed eight directed acyclic graphs to represent how these variables might be related, guided by the expectation that constraints on independent breeding and female promiscuity may lead to sex-biased philopatry and influence which sex helps more (supplementary Figure 3). We translated each of these eight paths into a set of statistical models using the d-separation method (Shipley, 2000). D-separation specifies the conditional independencies in each path. If there is indeed no relationship between the two variables in the conditional independency, or if there is no relationship after controlling for other variables, then the resulting *P* value of the relationship between these variables will be high. Fisher's *C* statistic is used to combine the *P* values of the conditional independencies for each path. We compared the resulting *C* statistics from our eight paths using the *C*-statistic information criterion (CICc) (Shipley, 2000).

To build the relevant statistical models, we reduced our data set to include one effect size per species. Given that there are multiple effect sizes for some species in our data set, we averaged these to have a single estimate of the mean difference in helper effort between the sexes for each species. We further reduced our data set to include only species for which all data was available ($N_{species} = 20$; the species with all information present in supplementary Table 2). We arcsine and z transformed the proportion of broods with extra-pair paternity and the proportion of nests with helpers and we z transformed the mean difference in helper effort. We constructed the models using the 'pgls' (phylogenetic generalised least squares) function in the caper R package (Orme *et al.*, 2013) and accounted for phylogenetic uncertainty by running each model on the same 1000 trees used in the BPMMs and taking the average *P* value to calculate the *C* statistic for each path.

RESULTS

Sex differences in helping

Across species, male helpers invested more in helping behaviour on average than female helpers, although this difference was not statistically significant ($\beta = 0.14$, CI = -0.17 to 0.44; $N_{species} = 26$; $N_{effect\ sizes} = 97$). Sex differences in helping behaviour vary in both directions, both within and between species: investment in helping was consistently biased towards females or males in ten out of nineteen species in which there was more than one effect size calculated, whereas in the nine remaining species, the effect sizes were in mixed directions – in some cases females helped more while in other cases males helped more (Figure 1).



species	lower 95% CI	mean difference	upper 95% CI
Seychelles Warbler	-3.27	-1.72	-0.17
Apostlebird	-2.48	-1.47	-0.47
Seychelles Warbler	-2.88	-1.41	0.06
Seychelles Warbler	-2.87	-1.4	0.07
Grey-crowned Babbler	-2.28	-1.24	-0.19
White-throated Magpie-jay	-2.23	-1.18	-0.13
Acorn Woodpecker	-1.82	-1.12	-0.42
White-throated Magpie-jay	-2.04	-1.07	-0.11
Seychelles Warbler	-1.91	-1.01	-0.11
Yellow-billed Shrike	-2.52	-1.01	0.51
White-throated Magpie-jay	-2.46	-0.94	0.57
Seychelles Warbler	-2.14	-0.79	0.56
Rufous Treecreeper	-2.37	-0.72	0.93
Seychelles Warbler	-2.01	-0.68	0.66
Rufous Treecreeper	-1.58	-0.62	0.33
Bell Miner	-1.44	-0.62	0.2
Rufous Treecreeper	-1.7	-0.61	0.49
White-throated Magpie-jay	-1.76	-0.56	0.64
Grey-crowned Babbler	-1.68	-0.52	0.64
Acorn Woodpecker	-1.71	-0.51	0.68
Acorn Woodpecker	-1.88	-0.48	0.92
Brown Jay	-0.96	-0.46	0.04
Laughing Kookaburra	-1.39	-0.41	0.57
Laughing Kookaburra	-2.01	-0.39	1.22
Acorn Woodpecker	-1.54	-0.36	0.83
Acorn Woodpecker	-0.97	-0.35	0.27
Laughing Kookaburra	-1.96	-0.34	1.27
Stripe-backed Wren	-1.1	-0.29	0.52
Stripe-backed Wren	-1.62	-0.27	1.08
Bell Miner	-1.13	-0.25	0.64
Brown Jay	-0.73	-0.24	0.25
Seychelles Warbler	-1.53	-0.24	1.06
Splendid Fairywren	-2.06	-0.23	1.61
Acorn Woodpecker	-0.84	-0.22	0.4
Apostlebird	-0.94	-0.21	0.51
Acorn Woodpecker	-0.96	-0.2	0.57
Galapagos Mockingbird	-0.63	-0.19	0.25
Green Woodhoopoe	-1.33	-0.17	0.99
Galapagos Mockingbird	-1.09	-0.15	0.8
Bell Miner	-1.03	-0.15	0.74
Bell Miner	-0.93	-0.12	0.69
Acorn Woodpecker	-0.64	-0.1	0.45
Acorn Woodpecker	-0.71	-0.1	0.52
Brown Jay	-0.62	-0.07	0.48
Stripe-backed Wren	-1.23	-0.05	1.14
Laughing Kookaburra	-1.37	-0.04	1.3
Red-winged Fairywren	-0.36	-0.02	0.32
Green Woodhoopoe	-1.24	0.02	1.29
Laughing Kookaburra	-1.55	0.05	1.66
Arabian Babbler	-1.15	0.06	1.27
Acorn Woodpecker	-0.55	0.06	0.68
Florida Scrub-jay	-1.76	0.07	1.89
Red-winged Fairywren	-0.78	0.16	1.11
Stripe-backed Wren	-0.77	0.17	1.11
Arabian Babbler	-0.44	0.2	0.84
Jungle Babbler	-0.65	0.22	1.09
Laughing Kookaburra	-1.12	0.22	1.56
Bell Miner	-1.21	0.23	1.67
El Oro Parakeet	-0.66	0.24	1.14
White-winged Chough	-1.08	0.27	1.62
Bell Miner	-0.48	0.28	1.04
Purple-crowned Fairywren	-0.32	0.29	0.91
Apostlebird	-0.47	0.33	1.13
Bell Miner	-0.4	0.36	1.12
Laughing Kookaburra	-0.96	0.39	1.73
Arabian Babbler	-0.41	0.42	1.26
Bell Miner	-1.01	0.43	1.87
Bell Miner	-0.12	0.46	1.03
Stripe-backed Wren	-0.72	0.46	1.63
Acorn Woodpecker	-0.93	0.46	1.86
Acorn Woodpecker	-0.69	0.5	1.7
Arabian Babbler	-0.1	0.55	1.2
Sociable Weaver	-0.28	0.57	1.41
Laughing Kookaburra	-0.19	0.59	1.36
Arabian Babbler	-0.65	0.6	1.84
Florida Scrub-jay	-1.28	0.61	2.5
Grey-backed Fiscal Shrike	-0.55	0.64	1.82
Laughing Kookaburra	-0.34	0.66	1.65
White-winged Chough	-0.73	0.66	2.04
Arabian Babbler	-0.17	0.68	1.53
Florida Scrub-jay	-0.43	0.72	1.87
Laughing Kookaburra	-0.26	0.74	1.74
Green Woodhoopoe	-0.12	0.74	1.6
Rufous Treecreeper	-0.53	0.74	2.01
Stripe-backed Wren	-0.48	0.76	2.01
Superb Starling	0.43	0.83	1.23
Carrion Crow	0	0.85	1.7
Grey-backed Fiscal Shrike	0	0.86	1.72
Grey-backed Fiscal Shrike	-0.22	0.89	2
Florida Scrub-jay	-0.25	0.93	2.11
Carrion Crow	-0.42	1.19	2.81
Red-winged Fairywren	-0.86	1.22	3.3
Rufous Treecreeper	0.46	1.35	2.23
Yellow-billed Shrike	0.09	1.4	2.71
Blue-breasted Fairywren	0.17	2	3.82
Florida Scrub-jay	0.49	3.39	6.29
Florida Scrub-jay	0.91	4.46	8.02

Figure 1. The variation in helping effort between the sexes across species. Points indicate the mean difference in helping effort and are bracketed by their 95% confidence intervals. Negative values indicate that females help more than males while positive values indicate that males help more than females.

There was a statistically significant difference in helping between the sexes in only 13 of the 97 effect sizes – seven female biased and six male-biased. The average number of individual females and males studied to calculate each effect size were 9.4 and 17.9 respectively, resulting in low statistical power, which may partly explain statistical support for equal investment between sexes in most species.

Sex differences in helping are explained by philopatry

We found that the difference in helping effort between the sexes was significantly associated with sex-biased philopatry (β = 0.73, CI = 0.29 to 1.15, $N_{species}$ = 20, $N_{effect\ sizes}$ = 83; Figure 2*a*). Philopatric females help more than males and philopatric males help more than females.

Contrary to the prediction that female promiscuity leads to male biased helping, females helped significantly more than males as the proportion of broods with extra-pair paternity increased (β = -0.21, CI = -0.39 to -0.01, $N_{species}$ = 20, $N_{effect\ sizes}$ = 83; Figure 2*b*). These results remained unchanged when we modelled: (1) the relationship between the mean difference in helper effort and philopatry independently of promiscuity, and (2) the relationship between the mean difference in helper effort and promiscuity independently of philopatry (see the legends of Figures 2*a* and 2*b* for parameter estimates).

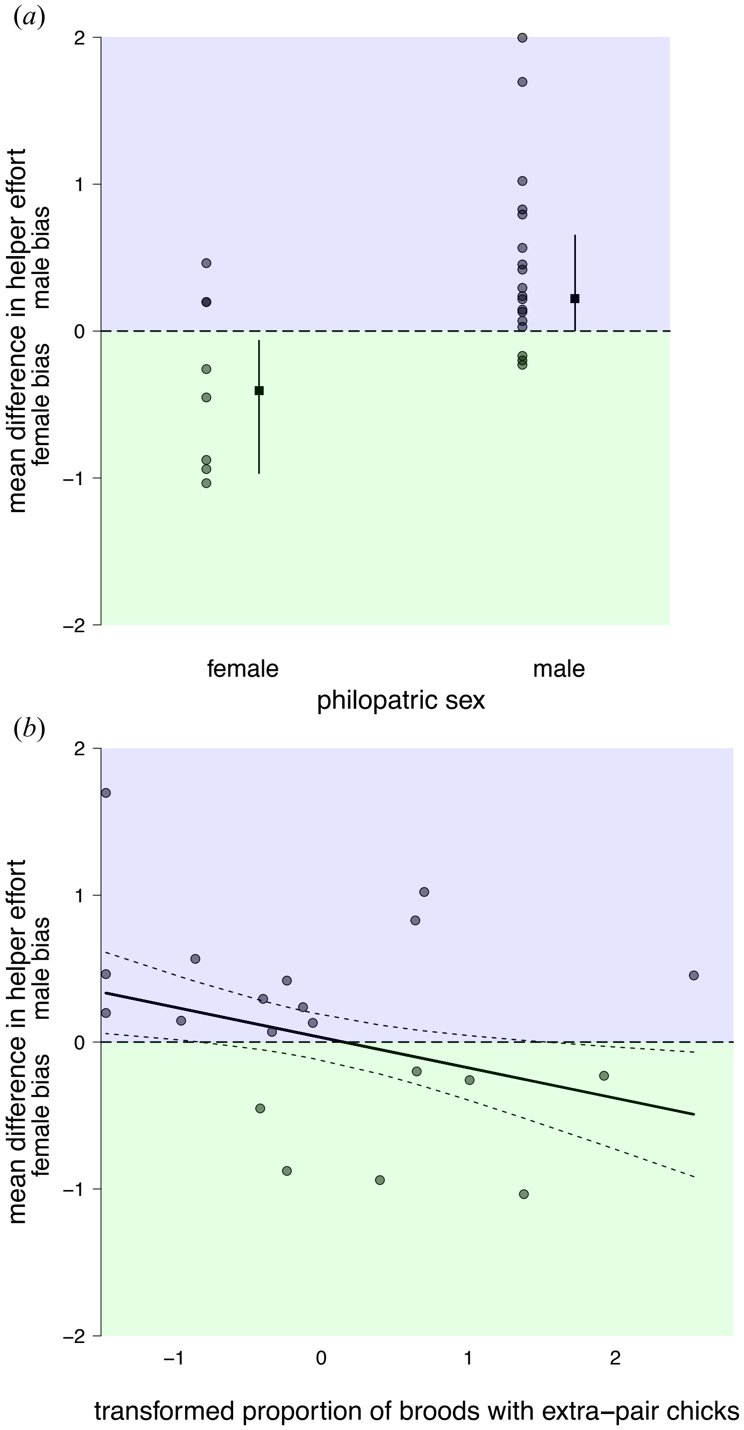


Figure 2. The mean difference in helper effort between the sexes and philopatry and female promiscuity. *(a)*, Females helped more when they were philopatric while males helped more when they were philopatric (*difference* = 0.75, CI = 0.33 to 1.20; $N_{species}$ = 26; $N_{effect\ sizes}$ = 97). Species averages are shown (circles) with the mean value (square) and the 95% credible interval beside the raw data. (*b)*, Females helped more than males as the proportion of broods with extra-pair chicks increased (*slope* = -0.20, CI = -0.46 to 0.02; $N_{species}$ = 20; $N_{effect\ sizes}$ = 83). Species averages are plotted along with the regression line and 95% credible intervals.

Sex-biased philopatry is explained by constraints on independent reproduction

The direction of sex-bias in philopatry was significantly associated with constraints on independent reproduction (β = -0.18, CI = -0.07 to -0.40, $N_{species}$ = 25; Figure 3). Specifically, the probability that males are philopatric decreased as the proportion of nests with helpers increased, indicating that when males are philopatric, cooperative breeding is typically facultative whereas when females are philopatric it is typically obligate.

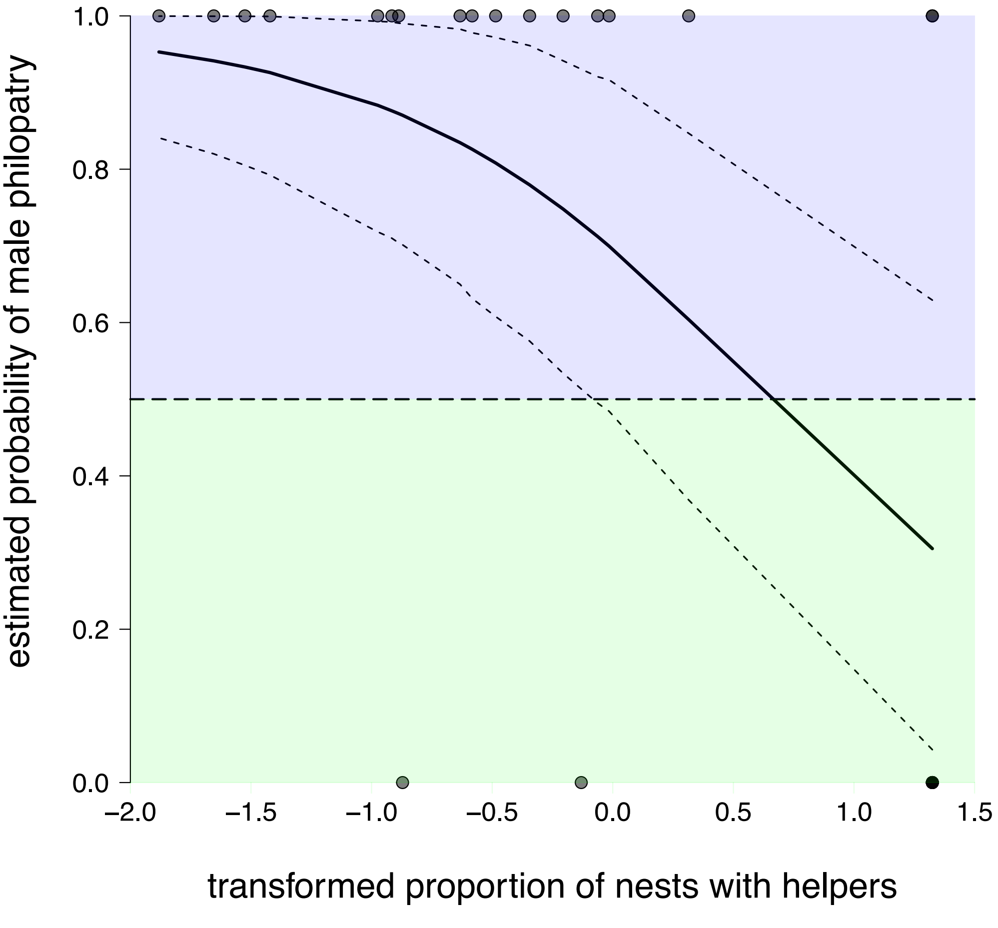


Figure 3. The probability that males are philopatric decreases as constraints on independent reproduction, measured as the proportion of nests with helpers, increase, indicating that females are philopatric when constraints on independent reproduction are high. Species with male philopatry are plotted at y = 1 while species with female philopatry are plotted at y = 0. The logistic regression line and 95% credible intervals are shown.

Evolutionary trajectory of sex differences in helping

A direct effect of constraints on independent reproduction on the direction of sex-bias in philopatry, and direct effects of the direction of sex-bias in philopatry and female promiscuity on the difference in helping effort between the sexes was the best-supported model of causal relationships between sex differences in helping, sex-biased philopatry, female promiscuity and constraints on independent reproduction (C = 1.7, df = 8, P = 0.99; supplementary Table 3). These results are consistent with the findings of our BPMMs supporting the hypothesis that females are philopatric when constraints on independent reproduction are high and that females help more than males when they are philopatric. The model that received the least support in our analysis excluded an effect of philopatry on the difference in helper effort (C = 20.6, df = 8, P = 0.01), further emphasising the importance of future direct fitness benefits in explaining helper investment in cooperative behaviour.

DISCUSSION

Variation in helper investment between the sexes across species of cooperative breeders provides a natural “controlled experiment" for distinguishing the importance of future direct fitness effects on the evolution of helping. By exploiting this variation in a series of comparative analyses, we show here that differences in investment between helpers are explained not by relatedness but by strategies designed to maximise the chance of breeding successfully in the future as a dominant breeder. The sex that remains to breed in its natal group, and whose future reproductive success is, therefore, more dependent on the future success of its natal group, typically helps more than the dispersing sex. This pattern is consistent with the hypothesis that investment in helping is at least partly determined by future direct fitness. In further analyses, we show that the direction of sex bias in philopatry is associated with constraints on independent reproduction – the probability of female philopatry increases as the proportion of nests with helpers increases. Cooperative breeding is typically obligate when philopatry is female biased, whereas it is usually facultative when philopatry is male biased. Taken together, these results suggest that female helping in cooperatively breeding birds is driven by a low probability of successfully dispersing to breed.

Indirect fitness benefits have played a key role in the evolution of cooperative systems (Boomsma, 2007; Hughes *et al.*, 2008; Cornwallis *et al.*, 2010; Lukas & Clutton-Brock, 2012a; Fisher *et al.*, 2013). However, our results indicate that helpers face a trade-off between indirect fitness benefits from helping related young in the natal nest, and potential future direct fitness benefits from dispersing to breed elsewhere. This trade-off in investment in current indirect versus future direct fitness is known to shape helping behaviour in other taxa. In two cooperatively breeding wasps where members of social groups are often sisters, the hairy-faced hover wasp, *Liostenogaster flavolineata*, and the paper wasp, *Polistes dominulus*, helpers next in line to inherit a breeding position reduce their investment in helping compared to helpers that have a low probability of acquiring a breeding position (Cant & Field, 2001; Field *et al.*, 2006). Therefore, across disparate taxa, future fitness considerations drive variation in the value that helpers place on indirect fitness benefits.

We did not find any support for the female promiscuity hypothesis (Charnov, 1981). The trend we detected was in fact in the opposite direction to that predicted: females helped more than males as promiscuity increased. Why don't males help more than females when the breeding female is promiscuous? One reason may be that a key assumption of the promiscuity hypothesis – that female promiscuity reduces breeding success for her mate – doesn't hold. Previous work has shown that extra-pair males are typically breeding males in other groups, with subordinate males gaining little direct fitness (Downing *et al.*, 2015). If breeding males in other groups are the extra-pair fathers then the direct fitness benefits of being a breeder are not different between the sexes (Queller, 1997). That is, breeding males enjoy the same amount of direct fitness as breeding females, just not in their own groups.

The prediction that the philopatric sex should help more is based on the assumption that, on average, philopatric helpers go on to breed in their natal territories (Kokko *et al.*, 2001). While this is true for some of the species in our analysis, for example in green woodhoopoes, *Phoeniculus purpureus*, it is not true in others, such as in laughing kookaburras, *Dacelo novaeguineae* (Plessis, 1992; Legge & Cockburn, 2000). Such cases may have obscured the effect we have managed to detect, however, in the case of the kookaburra at least, most new territories are established when a helper annexes a portion of its natal territory in which it goes on to breed (Legge & Cockburn, 2000). Such hidden benefits to philopatry may drive the effects we have detected even in the absence of inheritance of the dominant breeding position.

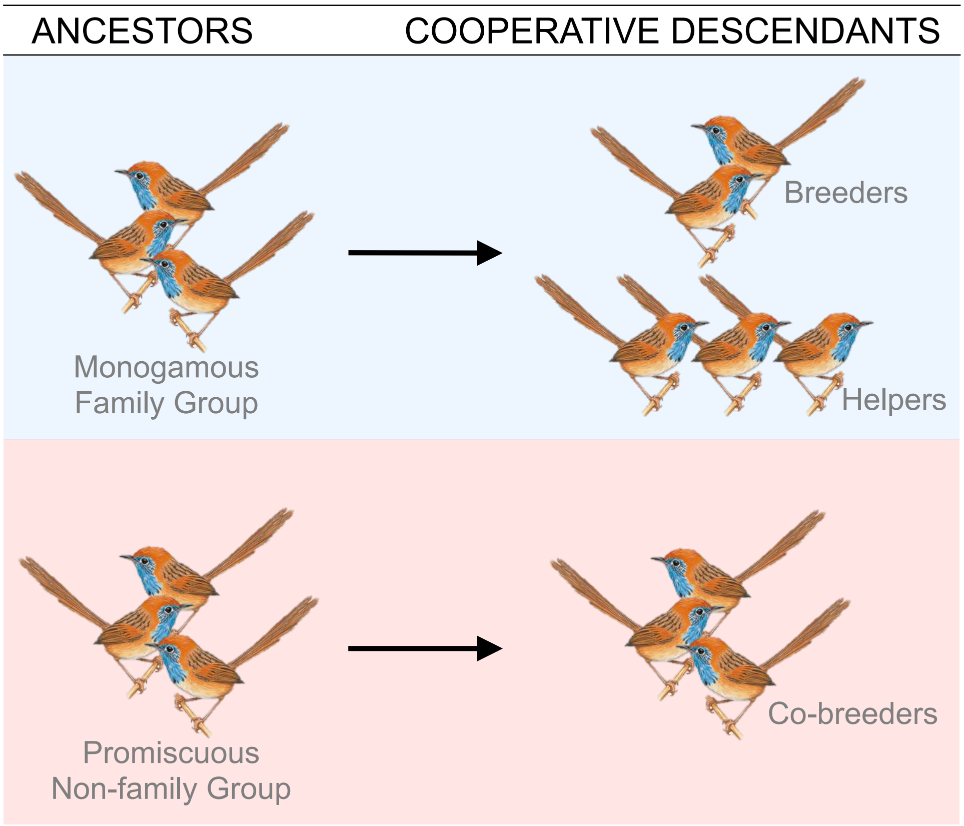
Divisions of labour between the sexes could result in biased estimates of helper effort. Divisions of labour are known to occur in some cooperatively breeding vertebrates.

For example in meerkats, *Suricata suricatta*, males contribute more to digging and guarding than females while females contribute more to babysitting and pup feeding than males (Clutton-Brock *et al.*, 2002). Such divisions of labour between the sexes can be even more extreme. In some termites species the soldier caste is often male while both sexes act as workers (Wilson, 1971). Our ability to detect a strong effect of philopatry on helping behaviour suggests that it has an overriding effect despite the division of labour between the sexes that may exist.

To conclude, our results are consistent with the hypothesis that future direct fitness benefits shape investment in cooperative behaviour. In cooperatively breeding birds, females help more than males when they are the philopatric sex and philopatry is female biased when constraints on independent reproduction are high. This suggests that the transition from facultative to obligate cooperative breeding in birds is driven by the increasing costs of dispersal to females. Female helpers also appear to care more for their siblings than male helpers as rates of extra-pair paternity increase. This trend is in the opposite direction to that predicted. One possibility is that in obligate cooperative breeders, reduced investment in raising siblings in response to increased extra-pair paternity results in fewer future helpers and therefore reduced future reproductive success of current helpers. In contrast, in facultative cooperative breeders, it is sometimes possible to raise young without the help of others. Whether this is the case remains to be determined.

Chapter 5

Evolutionary Transitions To Cooperative Breeding In Family And Non-Family Groups



ABSTRACT

Cooperatively breeding groups are typically family units formed through the retention of adult offspring that act as non-breeding helpers. This breeding system is more likely to evolve from species where breeders are monogamous as this increases relatedness between family members and therefore the kin selected benefits of cooperation. However, in many cooperatively breeding species, group members are unrelated, suggesting that monogamy fails to provide a general explanation for the evolution of cooperative breeding. Cooperative breeding in non-family groups may be an important precursor to cooperative breeding in family groups, which would suggest that changes in monogamy follow the origin of cooperative breeding rather than drive it. This prediction remains untested. By reconstructing ancestral states of breeding system and rates of female polyandry for 333 bird species, we present evidence to show that cooperative breeding in non-family and family groups result from distinct and non-overlapping evolutionary trajectories. In non-family groups, levels of ancestral polyandry did not influence the likelihood of cooperative breeding evolving. Furthermore, transitions to cooperative breeding in non-family groups result in relatively small social groups of co-breeders while there is a reproductive division of labour in family groups (meaning that only some individuals breed and others help to raise offspring). Overall, these results provide an explanation for the diversity of cooperative breeding systems seen in nature and emphasise the importance of distinguishing between different types of kin structure when making and testing predictions about the evolution of cooperative behaviour.

INTRODUCTION

A key step in the evolution of complex sociality is for individuals to join together and reproduce cooperatively in groups (Queller & Strassmann, 2009; Bourke, 2011; West *et al.*, 2015). The challenge is to explain why helping another individual to raise young is a better strategy for transmitting genes to future generations than breeding independently (Hamilton, 1963). Theoretical and empirical evidence show that genetic monogamy in family groups provides a unifying explanation for the evolution of helping behaviour across taxa (Boomsma, 2007; Hughes *et al.*, 2008; Boomsma, 2009; Cornwallis *et al.*, 2010; Lukas & Clutton-Brock, 2012a). The logic is that monogamy increases the kin selected benefits of helping because relatedness to full siblings and own offspring are equivalent (r = 0.5 on average). In many species however, unrelated individuals form groups and cooperate in raising young, which challenges monogamy as an explanation for the evolution of cooperative breeding since factors other than relatedness can clearly make helping worthwhile.

Cooperative breeding is usually considered to be a single breeding strategy with species placed in relation to one another along a continuum of reproductive skew (Stacey & Koenig, 1990; Sherman *et al.*, 1995; Cockburn, 1998; Jetz & Rubenstein, 2011). Family groups are at one end of this continuum and non-family groups are at the other. However, empirical work testing whether monogamy drives evolutionary transitions to cooperative breeding only considered family groups (Hughes *et al.*, 2008; Cornwallis *et al.*, 2010; Lukas & Clutton-Brock, 2012a). By treating cooperative breeding in family groups as a separate breeding system, it is possible that the direction of causality inferred by these studies between monogamy and cooperative breeding is wrong. Specifically, it may be that specific combinations of ecological parameters make the benefits of cooperating high and the costs low, favouring transitions to cooperative breeding independently of relatedness within social groups. This is feasible – cooperative breeding in birds is correlated with harsh environmental conditions and with the distribution of obligate brood parasites (Jetz & Rubenstein, 2011; Feeney *et al.*, 2013). Once cooperative breeding has evolved, changes in ecological conditions may then favour transitions to family based cooperation and monogamy (Cockburn, 2013; Dillard & Westneat, 2016). Ignoring non-family groups would place the origin of cooperation after changes in monogamy rather than before. In order to determine whether cooperative breeding in non-family groups preceded cooperative breeding in family groups, we need to reconstruct the origins of cooperative breeding in family and non-family groups.

Cooperatively breeding species also vary in their social complexity. This variation is predicted to depend on relatedness (Bourke, 2011; Fisher *et al.*, 2013; West *et al.*, 2015). Specifically, the trend towards large societies with specialised breeders and helpers is only predicted in family groups. In monogamous family groups, relatedness to siblings is the same as relatedness to own offspring which allows for a reproductive division of labour. In contrast, members of non-family groups are expected to be co-breeders, limiting specialisation to non-reproductive roles. Furthermore, group size is likely to be larger in families than it is in non-families: in family groups a helper's relatedness to the brood does not change with increasing groups size whereas in non-family groups a helper's relatedness to the brood decreases with each extra group member (Hartley & Davies, 1994). Relatedness is yet to be used to account for differences in the levels of sociality observed in cooperatively breeding species.

Birds are a unique group in which these predictions can be tested: cooperative breeding occurs in both family and non-family groups, the mating systems of over 300 species have been genetically determined and the phylogenetic relationships among species are well resolved (Cockburn, 2006; Jetz *et al.*, 2012). We take advantage of this knowledge and use phylogenetic comparative analyses to explain the diversity of cooperative breeding systems. We test if there are distinct evolutionary routes to cooperative breeding in family and non-family groups, if different selective pressures favour their origins and if family groups are more socially complex than non-family groups. Specifically, we use a combination of stochastic character mapping, phylogenetic mixed models and reverse jump Markov chain Monte Carlo models to reconstruct ancestral breeding systems and polyandry rates, to compare rates of reproductive sharing in family and non-family groups and to examine how large these groups are.

METHODS

Data Collection

Breeding System

We assigned all species of bird whose breeding systems have been genetically determined ($N_{species}$ = 333; Supplementary Table 1) into one of three categories: species that breed cooperatively in non-family groups ($N_{species}$ = 16), species that breed cooperatively in family groups ($N_{species}$ = 45) and species that do not breed cooperatively ($N_{species}$ = 272). These include the species analysed by Cornwallis *et al.* (2010) and all studies reporting polyandry rates in birds published up to and including the 10th of March 2016. Species were assigned as non-family cooperative breeders if groups form when unrelated individuals come together, and as family cooperative breeders when offspring delay dispersal to help. In six species in our data set, groups form when related individuals come together, typically after failed breeding attempts ('redirected helper' [1] in Supplementary Table 1). These were treated as non-cooperative in our analyses since the predictions we are testing concern family groups that form when individuals stay together and groups of unrelated individuals that come together. We compared these assignments with those made by Riehl (2013) who provided a categorization of avian cooperative breeding systems. Our 'non-family' category corresponds to Riehl's 'groups contain only unrelated co-breeders' category, while our 'family' category corresponds to Riehl's other three categories. In only four cases did these assignments disagree: we assigned *Guira guira*, *Porphyrio porphyrio, Pseudopodoces humilis* and *Upupa epops* as non-family cooperative breeders whereas Riehl assigned this species as showing some kin structure in their groups.

Sources of Extra-pair Paternity

We compiled data on the proportion of broods with extra-pair paternity for the 333 bird species in our data set. In cooperatively breeding birds there are two sources of extra-pair paternity: within-group extra-pair paternity where 'non-pair' males within the social group sire young and extra-group paternity where males outside the social group sire young. In non-cooperative species the pair can be thought of as the group,

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[1] This is a weird breeding system. See Figure A1 included at the end of this chapter.

meaning that within-group extra-pair paternity and extra-group paternity are equal. We were able to determine if the extra-pair chicks within a brood were sired by within-group or extra-groups males for 14 of the 16 non-family cooperative breeders and for 34 of the 45 family cooperative breeders in our data set (Supplementary Table 2). We only included broods in which mixed paternity was possible to detect in these estimates: broods cared for by at least two males and in which at least two offspring were genotyped. We do not consider a brood with extra-group young to have mixed within-group paternity unless it also contains young fathered by different within-group males. We used this data to answer two questions: we reconstructed ancestral polyandry rates measured as the proportion of broods with extra-pair paternity and we tested whether non-family group members are co-breeders while there is a reproductive division of labour in family groups.

Group Size

We searched the published literature for data on mean group size for the 61 cooperative species in our data set. In total, we obtained estimates of mean group size for 59 of these species (Supplementary Table 3).

Phylogenetic Trees

We used the phylogenetic trees published by Jetz *et al.* (2012) for our ancestral state reconstructions and to account for non-independence between species due to shared evolutionary history. We created ten trees ($N_{species} = 333$), each a maximum clade credibility (MCC) consensus tree constructed from 1000 posterior samples from the

Jetz *et al*. study using Tree Annotator v.2.0.3 (Drummond *et al.*, 2012), to account for phylogenetic uncertainty. The way we integrated the results obtained from these different trees depended on the method being used. For the stochastic character mapping and BayesTraits analyses the model is applied to the ten MCC trees simultaneously. For the Bayesian Phylogenetic Mixed Models (BPMMs), the model is applied to each tree in turn and therefore we combined the posterior samples from each tree prior to parameter estimation. Since the number of species for which we had data available differed depending on the analysis being performed, we used the APE R package (Paradis *et al.*, 2004) to trim the MCC trees to include only species for which we had data (see the supplementary R script for further details).

ANALYSES

Evolutionary Routes to Cooperative Breeding

To test if cooperative breeding in family and in non-family groups are distinct evolutionary routes to cooperative breeding we estimated ancestral breeding systems on each of the ten MCC trees. We used three complimentary approaches. First, we used stochastic character mapping to determine the number and direction of evolutionary transitions between family, non-family and non-cooperative breeding systems. This approach models changes between the three breeding systems as a continuous-time reversible Markov model allowing all possible character histories to be considered, thereby incorporating uncertainty in ancestral states. We built 100 stochastic character maps for each of the ten MCC trees using an equal rates model in the ‘phytools’ R package (Revell, 2011).

Second, we reconstructed ancestral states of breeding system using BPMMs in the ‘MCMCglmm’ R package (Hadfield & Nakagawa, 2010). We reconstructed ancestral states of non-family and family cooperative breeding separately by fitting breeding system as a binary response variable (non-family vs. non-cooperative in the first model and family vs. non-cooperative in the second model) with only the intercept as a fixed effect. Including a phylogenetic covariance matrix as a random effect estimates the probability that each node of a phylogeny is cooperative. For the non-family reconstructions, we classified each ancestral node as non-family if the posterior probability was ≥ 0.95 and as non-cooperative if the posterior probability was ≤ 0.05. For the family reconstructions, we classified each ancestral node as family if the posterior probability was ≥ 0.95 and as non-cooperative if the posterior probability was ≤ 0.05. We treated any ancestral nodes with probability > 0.05 and < 0.95 as unknown. We then combined the separate ancestral state reconstructions into a single transitions data frame. If both reconstructions unambiguously assigned a given node as non-cooperative, this node was assigned as non-cooperative. Any unknown nodes in one set of reconstructions but known in the other were assigned the state of the known reconstruction. All non-family nodes assigned as non-cooperative in the family reconstructions were assigned as non-family. All family nodes assigned as non-cooperative in the non-family reconstructions were assigned as family. Any ambiguous nodes, those predicted to be non-kin in one set of reconstructions and kin in the other, were treated as ‘both’. The resulting transitions data frame consists of the ancestor and descendant of each node of a phylogeny. Combining ancestors and descendants gives nine possible evolutionary transitions: a non-family ancestor with a i) non-family, ii) family or iii) non-cooperative descendant; a non-cooperative ancestor with a iv) non-family, v) family or vi) non-cooperative descendant; a family ancestor with a vii) non-family, viii) family or ix) non-cooperative descendant. These ancestral state reconstructions were used to calculate the frequencies of the nine different types of transition.

Third, we used reverse jump Markov chain Monte Carlo (rjMCMC) in the multi-state module in BayesTraits v2.0 (Pagel & Meade, 2006) to compare different models of the evolutionary routes to cooperative breeding[2]. We constructed four models of trait evolution: i) a model where gains and losses of cooperative breeding in family and non-family groups and transitions between these occurred at an equal rate, ii) a model where transitions between cooperative breeding in family and non-family groups were restricted, iii) a model where gains and losses of cooperative breeding in family groups could only happen from ancestors that bred cooperatively in non-family groups and iv) a model where gains and losses of cooperative breeding in non-family groups could only happen from ancestors that bred cooperatively in family groups. We calculated the harmonic mean of each model, an estimate of its marginal likelihood, and tested the fit of the best model against the three alternative using Bayes Factors (2 x (log-likelihood of complex model – log-likelihood of simple model)). Bayes factors greater than 2 suggest ‘positive evidence’ of a difference between the models, Bayes factors greater than 5 suggest ‘strong evidence’ and Bayes factors greater than 10 suggest ‘very strong evidence’ of a difference. Each model was run for 6,000,000 iterations with the first 1,000,000 iterations discarded and then

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[2] See Figure A2 at the end of this chapter for examples of the kind of model that can be built.

sampled every 5,000 iterations. We used a hyper-prior to seed the mean of the exponential prior from a uniform distribution between 0 and 30 in each model.

Ancestral polyandry

To compare levels of polyandry in the ancestors of non-family groups against levels of polyandry in the ancestors of family groups and non-cooperative species we constructed a BPMM with the proportion of broods with at least one extra-pair chick as the response variable (using a binomial error distribution with a logit link function) and the nodal classifications from the ancestral state reconstructions done above using BPMMs as the explanatory variable (a factor with nine levels). We specified the ancestors in our transition data frame as a random effect to estimate ancestral values of polyandry for each of the nine transitions categories. Treating the transition categories as a fixed effect assumes that these are measured without error. However, each ancestral estimate is associated with a degree of uncertainty. To account for this, we estimated ancestral breeding states 100 times, each time reclassifying each node by re-sampling from the posterior distribution of the probability of each node being cooperative. The resulting posterior samples from the 100 repeats were then combined.

Reproductive division of labour

We tested whether members of non-family groups are co-breeders while there is a reproductive division of labour in family groups by comparing levels of within-group extra-pair paternity and extra-group paternity between species that breed cooperatively in non-family and family groups. If group members are co-breeders we would expect high levels of within-group extra-pair paternity. If there is a reproductive division of labour we would expect low levels of within-group extra-pair paternity. We constructed a multi-response BPMM with the proportion of broods with within-group extra-pair paternity and the proportion of broods with extra-group paternity as response variables (using a binomial distribution with a logit link function for each) with breeding system (two level factor: non-family cooperative breeder vs. family cooperative breeder) included as a fixed effect and a phylogenetic covariance matrix included as a random effect to account for non-independence between species due to shared ancestry.

Group Size

To determine if group size is larger in species that breed cooperatively in family groups than it is in species that breed cooperatively in non-family groups, we constructed a BPMM with mean group size (rounded to the nearest integer; Poisson error distribution) as the response variable and breeding system (two level factor: non-family cooperative breeder vs. family cooperative breeder) as a fixed effect. We included a phylogenetic covariance matrix as a random effect to account for non-independence between species due to shared ancestry.

We report the equations for our models and details of the variance structures and priors used in these analyses in the supplementary R script. We examined plots of chain mixing and levels autocorrelation to assess model convergence. We report estimates of fixed effects (β) from our BPMMs on the original scale with 95%

credible intervals (CI). Our *P* values testing for differences between levels of a fixed effect are calculated from the posterior distribution of parameter estimates as the proportion of times that one level is greater than the other.

RESULTS

There are distinct evolutionary routes to cooperative breeding

There have been 15 transitions to cooperative breeding in non-family groups and 28 transitions to cooperative breeding in family groups (Figure 1). All of these transitions occurred from non-cooperative ancestors (Figure 2; these are the average number of transitions based on the results of the stochastic character mapping and the ancestral state reconstructions using BPMMs, across the 10 MCC trees). There have only been two transitions between cooperative breeding in family and non-family groups. The ancestor of the subdesert mesite, *Monias benschi*, bred cooperatively in non-family groups and the ancestor of the purple swamp hen, *Porphyrio porphyrio*, bred cooperatively in family groups. Furthermore, cooperative breeding has been lost seven times: five times from family groups and twice from non-family groups. We also found that the best model of the evolutionary routes to cooperative breeding was one where transitions between cooperative breeding in family and non-family groups could not happen (harmonic mean = -169.8). This model provided a marginally better fit to the data than one in which transitions between cooperative breeding in family and non-family groups occurred at an equal rate, estimated to be close to 0 (harmonic mean = -171.2, Bayes Factor = 2.8).

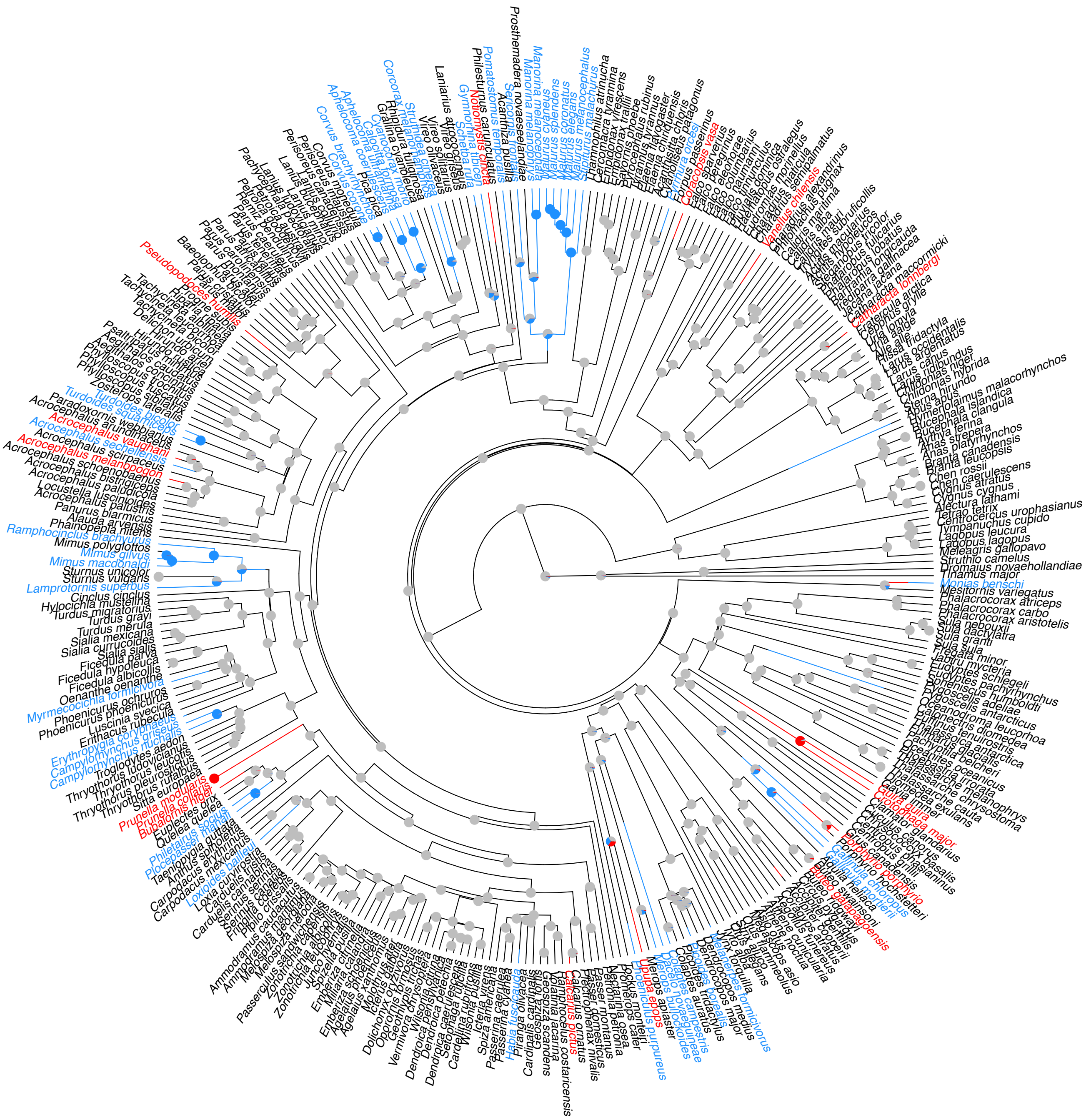


Figure 1. A stochastic character map of the distribution of cooperative breeding in non-family groups (red), family groups (blue) and non-cooperative breeding (black/grey). The pie charts at each node show aggregated posterior probabilities of each state across 100 stochastically mapped character histories using an equal rates model of evolution.

This model was also substantially better than a model where gains and losses of cooperative breeding in family groups could only happen from ancestors that bred cooperatively in non-family groups (harmonic mean = -191.3, Bayes Factor = 43.0) and one where gains and losses of cooperative breeding in non-family groups could only happen from ancestors that bred cooperatively in family groups (harmonic mean = -194.1, Bayes Factor = 48.6).

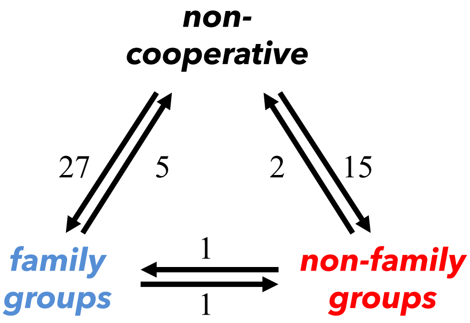


Figure 2. The estimated number of transitions between cooperative breeding in non-family groups, family groups and non-cooperative breeding based on 1000 stochastic character maps (100 for each of the ten MCC trees). Arrows represent the direction of transitions.

Non-family group members are co-breeders

Rates of extra-pair paternity were almost twice as high in the ancestors of species that breed cooperatively in non-family groups than in the ancestors of species that breed cooperatively in family groups (non-family group ancestral polyandry, $\beta = 0.39$, CI = 0.16 to 0.74; family group ancestral polyandry, $\beta = 0.22$, CI = 0.07 to 0.53; $P = 0.02$; $N_{species} = 333$; Figure 3). In contrast, extra-pair paternity was similar in the ancestors of non-family cooperative breeders and non-cooperative species (non-cooperative ancestral polyandry, $\beta = 0.47$, CI = 0.20 to 0.70; $P = 0.49$). Furthermore, extra-pair paternity was lower in the ancestors of species that breed cooperatively in family groups than in the ancestors of non-cooperative species ($P = 0.07$).

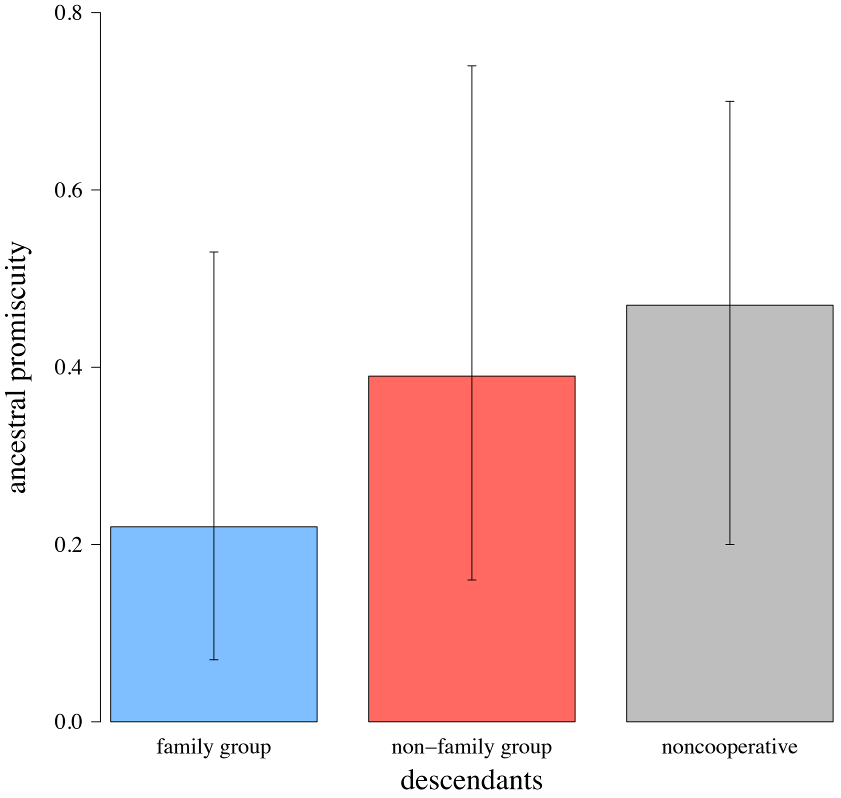


Figure 3. Female polyandry is significantly higher in the non-cooperative ancestors of species that breed cooperatively in non-family groups than it is in the ancestors of species that breed cooperatively in family groups. Data show the back transformed mode and Bayesian 95% credible interval of the posterior distribution of ancestral parameter estimates of female polyandry.

Within groups, paternity was shared significantly more in non-family groups compared with family groups (non-family group within-group extra-pair paternity β = 0.89, CI = 0.4 to 0.99, $N_{species}$ = 14; family group within-group extra-pair paternity β = 0.05, CI = 0.0002 to 0.45, $N_{species}$ = 34; $P < 0.0001$; Figure 4). There was no difference, however, in extra-group paternity between non-family and family groups which were both low (non-family extra-group paternity, β = 0.01, CI = 0.0002 to 0.21, $N_{species}$ = 14; family extra-group paternity, β = 0.01, CI = 0.0004 to 0.12, $N_{species}$ = 34; $P = 0.3$).

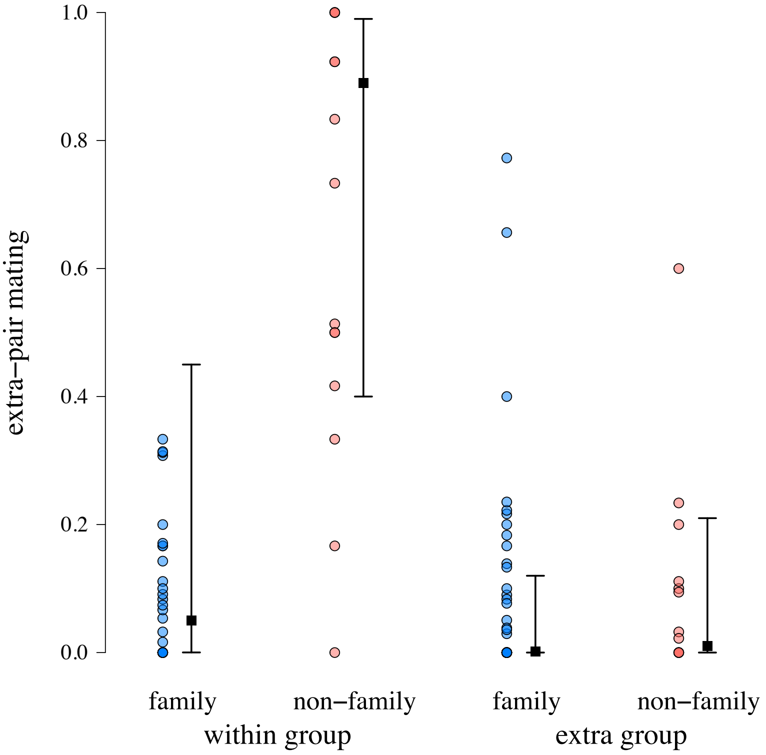


Figure 4. Within group extra-pair mating and extra-group extra-pair mating in species that breed cooperatively in family (blue) and non-family (red) groups. The raw data are plotted (circles) with the back transformed mode (square) and Bayesian 95% credible interval of the posterior distribution of parameter estimates plotted beside the raw data.

Group sizes are smaller in non-family groups

Cooperative group size was smaller in non-family groups than in family groups: on average, across cooperative species, non-family groups consisted of three individuals, while family groups consisted of four individuals (non-family group size $\beta = 2.60$, CI = 1.37 to 4.40, $N_{species} = 14$; family group size $\beta = 3.93$, CI = 1.90 to 5.78, $N_{species} = 59$; $P = 0.051$; Figure 5). Although mean group size only differs by one individual between family and non-family cooperative breeders, the largest mean group size of any species that breeds cooperative in non-family groups was 6.6 while it was 21 in family groups, consistent with the hypothesis that high relatedness and a reproductive division of labour leads to the evolution of larger group sizes.

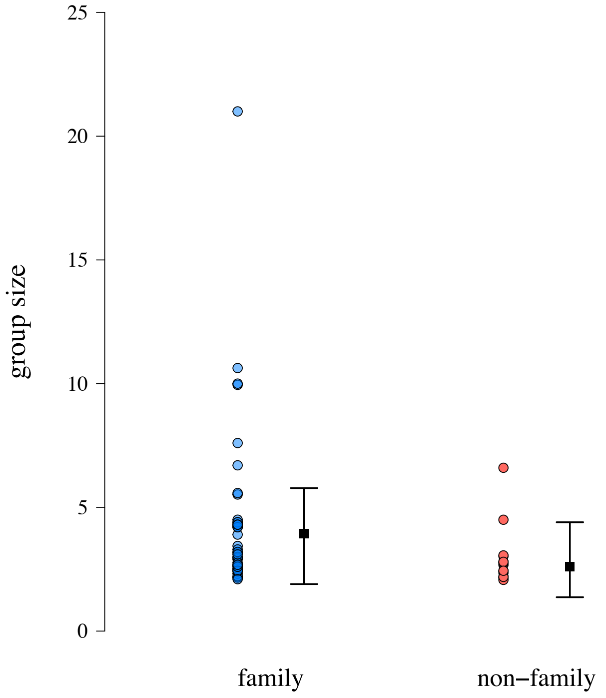


Figure 5. Group size was larger in cooperative species that breed in family groups (blue) than in non-family groups (red). The raw data are plotted (circles) with the back transformed mode (square) and Bayesian 95% credible interval of the posterior distribution of parameter estimates plotted beside the raw data.

DISCUSSION

Cooperative breeding in family and non-family groups results from distinct and non-overlapping evolutionary trajectories. Our results show that each breeding system evolves from non-cooperative ancestors and that the evolutionary forces driving transitions to cooperative breeding depend on relatedness within social groups. Polyandrous mating is associated with the evolution of cooperative breeding in non-family groups while monogamous mating makes the evolution of cooperative breeding in family groups more likely. Furthermore, cooperative breeding in non-family groups is maintained by shared reproduction while there is a reproductive division of labour in family groups. This difference leads to larger group sizes in family groups.

Part of the reason for the debate about importance of indirect versus direct fitness benefits in the evolution of cooperative breeding is because non-family and family based cooperative systems are often regarded as the same phenomenon (Stacey & Koenig, 1990; Sherman *et al.*, 1995; Cockburn, 1998; Jetz & Rubenstein, 2011). However, inclusive fitness theory predicts distinct evolutionary trajectories to cooperative depending on relatedness structure (Hamilton, 1964a; b; Bourke, 2011; Gardner *et al.*, 2011; West *et al.*, 2015). The monogamy hypothesis only predicts that lifetime monogamy will favour cooperative breeding in family groups by leading to maximal sibling relatedness. The monogamy hypothesis does not make predictions about the evolution of cooperative breeding in non-family groups. Our results confirm this and show that high relatedness does not provide a general explanation for the evolution of all cooperative breeding systems, only those composed of relatives.

In birds, transitions between cooperative breeding in non-family and family groups, while intuitively plausible, are rarely seen. We found that the ancestor of the subdesert mesite, *Monias benschi*, which breeds cooperatively in family groups was a non-family group cooperative breeder. This result is likely to reflect a limitation in stochastic character mapping as we did not recover this relationship using other methods of ancestral state reconstruction. We also found that the ancestor of the purple swamp hen, *Porphyrio porphyrio*, which breeds cooperatively in non-family groups, was a family group cooperative breeder. Interestingly, other authors have categorised this species as having some kin structure in its groups (Riehl, 2013). Further study of this species is required.

The rarity of transitions between cooperative breeding in non-family and family groups is surprising given that relatedness in family groups is often degraded by polyandry, mortality, divorce and immigration and therefore could feasibly lead to reproductive cooperation between non-relatives (Mulder *et al.*, 1994; Baglione, 2002; Warrington *et al.*, 2015). Similarly, ecological conditions may select for cooperative breeding among non-relatives but group living may become so advantageous that offspring are selected to delay dispersal, leading to family based cooperation (Cockburn, 2013). One possibility, which we did not explore in our analyses, is that 'redirected helping' systems represent a stepping-stone back to non-cooperative breeding from cooperative breeding in family groups. We will explore this option in future analyses.

The rarity of transitions between cooperative breeding in non-family and family groups in birds is consistent with the pattern found in Halictid bees (Danforth, 2002). Primitive eusociality has evolved independently from solitary ancestors three times and was not preceded by cooperative breeding in non-family groups. There is presently little theoretical evidence for why transitions between cooperative breeding in non-family and family groups are empirically unlikely but such theory would provide a useful basis for disentangling the origins of the diversity of social systems that appear to be replicated across very disparate taxa.

Cooperative breeding is an important step in the evolution of complex sociality (Queller & Strassmann, 2009; Bourke, 2011; West *et al.*, 2015). As seen, cooperative breeding in birds has evolved in both family and non-family groups. Further changes in complexity however have only been observed in family groups, as predicted from the monogamy hypothesis logic. Evidence for this comes from major evolutionary transitions to multicellularity from single-celled organisms: obligate and irreversible multicellularity has only ever evolved in taxa where groups are formed clonally (Fisher *et al.*, 2013). Evidence also comes from major evolutionary transitions to eusociality, where workers have developed lifetime unmatedness: this has only ever evolved where queens are singly mated, leading to full-sib relatedness between all her offspring (Hughes *et al.*, 2008). In both cases kin selection is maximally effective because there is no sexual conflict. Our results show that the lack of sexual conflict also leads to greater social complexity in birds. A reproductive division of labour is only observed in family groups and group sizes are larger on average than they are in non-family groups.

Overall, our results show that cooperative breeding in non-family and family groups evolve and are maintained by different selective forces. The evolutionary route followed to cooperative breeding has important consequences for the subsequent evolution of social complexity. Only in cooperatively breeding family groups do we observe a reproductive division of labour and large group size. These results are consistent with the predictions of inclusive fitness theory and provide a unifying explanation for the diversity of cooperative breeding systems observed in nature and for variation in the degree of social complexity across species.

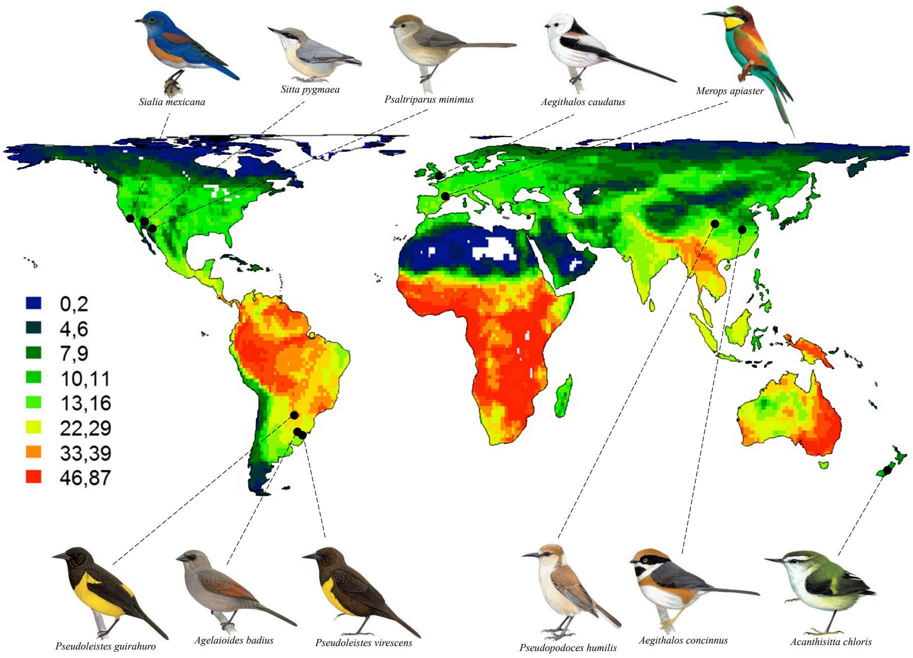


Figure A1. The distribution of ‘redirected helpers’ plotted onto the global distribution of all cooperative breeding birds (Jetz & Rubenstein, 2011). Note that all cases of redirected helping occur at the extreme latitudinal limits of cooperative breeding.

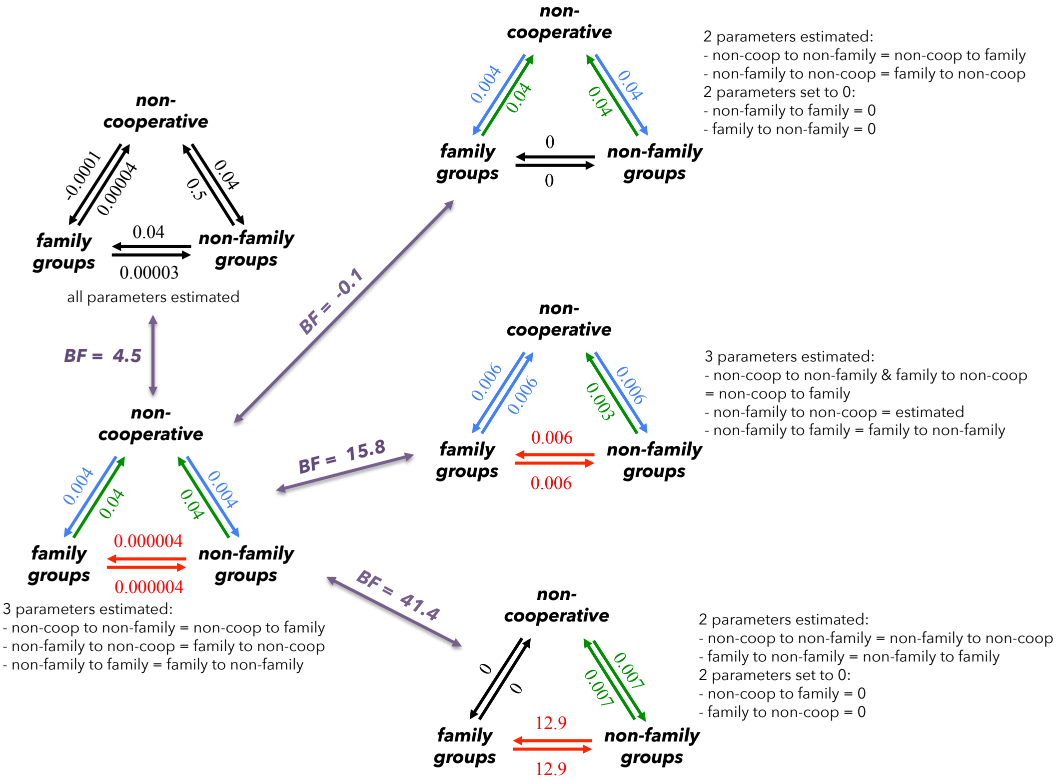
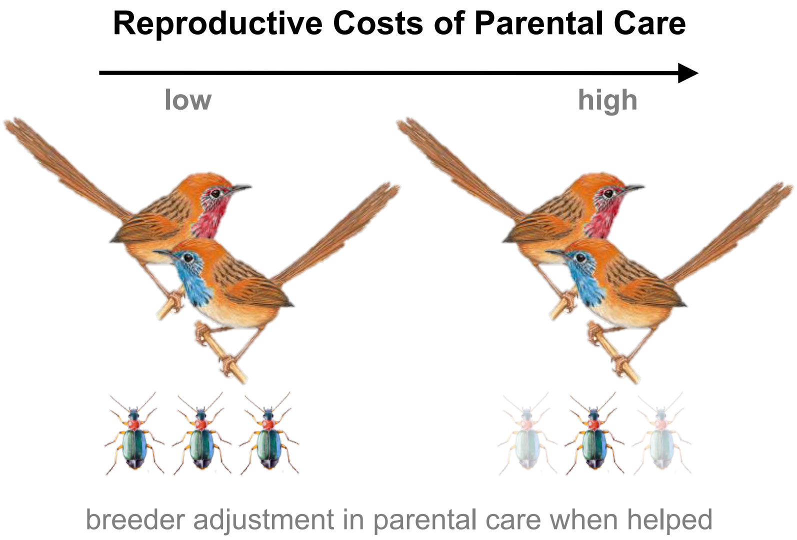


Figure A2. Examples of models built using BayesTraits.

Chapter 6

Provisioning Guidelines for Breeders in Cooperative Societies



ABSTRACT

Little empirical attention has been paid to how much breeders in cooperative societies should adjust their investment in parental behaviour when they have helpers at the nest. Breeders are predicted to reduce their investment when the costs of care are high and to maintain their investment when the costs of care are low. I test this prediction in facultative cooperatively breeding birds using adult survival to approximate the costs of care and a statistical effect size to estimate how much breeders adjust their effort in parental care when they have helpers at the nest. Using a phylogenetic meta-analytic approach, I found support for the expected positive relationship between reductions in parental care and adult survival in both male and female breeders. This supports the prediction that the reproductive costs of care shape investment by breeders in parental behaviour when they have helpers at the nest.

INTRODUCTION

In many cooperatively breeding birds, helping is facultative (Stacey & Koenig, 1990; Koenig & Dickinson, 2016). Some breeding pairs are assisted in offspring care by nonbreeding helpers while others are not. Contrasts between pairs with and without helpers show that in most species, female and male breeders reduce their investment in parental care when helped (Cockburn, 1998; Hatchwell, 1999). There are some species, however, in which neither sex adjusts its behaviour. Theory predicts that breeders should reduce their investment in offspring when the reproductive costs of care are high (Figure 1a), providing a potential explanation for variation in breeder adjustment (Crick, 1992; Hatchwell, 1999; Hardling *et al.*, 2003; Johnstone, 2011). However, this prediction has received little empirical attention.

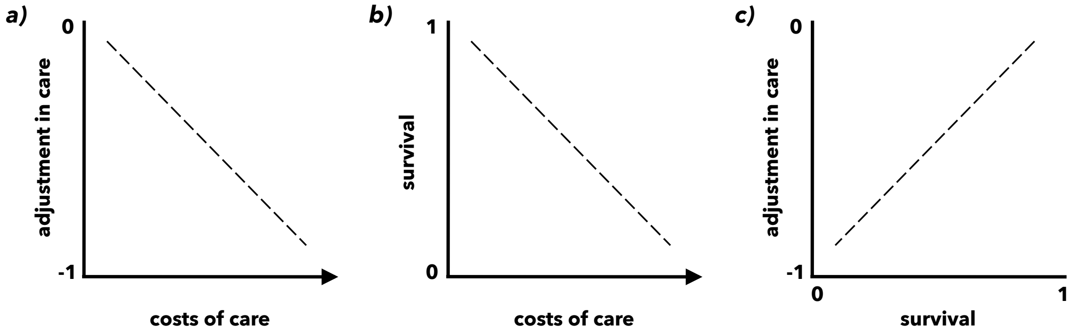


Figure 1. *a*) Breeders are predicted to reduce (< 0) their investment in parental care when the reproductive costs of caring are high and to maintain their investment when the costs of caring are low. *b*) Survival varies inversely with the costs of care. *c*) Low survival provides a proxy for high costs of care and should be associated with large reductions in parental care. High survival provides a proxy for low costs of care and should be associated no adjustment in parental care.

One difficulty in testing this prediction is that the reproductive costs of caring have rarely been quantified in cooperatively breeding birds (Ketterson & Nolan, 1994; Bennett & Owens, 2002; Cockburn, 2006). Furthermore, metrics of breeder investment in parental care are often species specific and therefore not comparable (McGowan & Woolfenden, 1990; Whittingham & Dunn, 1998; Browning *et al.*, 2012). For example, the total amount of food delivered to young, the hourly feeding rate and time spent incubating are commonly reported metrics. A solution to the first problem is to use the adult survival rate to approximate reproductive costs, as survival is likely to vary inversely with the costs of care (Figure 1b) (Hatchwell, 1999). The second problem can be resolved by translating different metrics of breeder investment in parental care into statistical effect sizes to make them comparable across species (Nakagawa & Cuthill, 2007; Nakagawa & Santos, 2012).

Here, I provide an empirical test of whether breeders reduce their investment in parental care when the reproductive costs of caring are high. I do so by using adult survival rates for females and males in cooperatively breeding birds to approximate the costs of caring for each sex. I also translate the difference in the amount that breeders care at helped and unhelped nests in cooperatively breeding birds into a statistical effect size for each sex separately to estimate adjustment. This allows me to use a phylogenetic meta-analytic approach to test for the expected positive relationship between reductions in parental care and adult survival (Figure 1c).

METHODS

Data Collection

I searched the published literature using Scopus and the Web of Knowledge for studies measuring breeder investment in parental care in cooperatively breeding birds. I used the following topic search term: '(feed* OR provision* OR help* OR defen*) AND species name'. I restricted my search to facultative cooperatively breeding species that live in family groups. This is because individuals that help in species that breed cooperatively in non-family groups follow different provisioning rules to helpers in family groups and this in turn will influence how breeders adjust their parental care when helped (Davies *et al.*, 1995a; b). I searched for studies on 110 species, those listed as breeding in family groups in Riehl's (2013) review of cooperative breeding in birds, using both common and scientific names. I extracted effect sizes using the Preferred Reporting Items for Systematic Reviews and Meta-Analysis statement (Liberati *et al.*, 2009; Moher *et al.*, 2009).

Effect Sizes

I calculated two effect sizes using Hedges' *d* (Nakagawa & Cuthill, 2007; Nakagawa *et al.*, 2014): how much the breeding female adjusts her parental care when helped (*Female Adjustment*) and how much the breeding male adjusts his parental care when helped (*Male Adjustment*):

$$Adjustment = ((X_{group} - X_{pair}) / S_{pooled}) * J$$

Where X_{group} is the mean breeder investment in parental care at helped nests, X_{pair} is the mean breeder investment in parental care at unhelped nests, S_{pooled} is the pooled standard deviation and J is a bias correction for small sample sizes (see the supplementary R script for more details). If the value of *Female Adjustment* or *Male Adjustment* is negative, breeders reduce their investment in parental care when helped. If the value of *Female Adjustment* or *Male Adjustment* is positive, breeders increase their investment in parental care when helped. In total, I was able to calculate 54 effect sizes (27 *Female Adjustment* and 27 *Male Adjustment*) from 17 studies representing 16 cooperatively breeding bird species (supplementary Table 1). In all cases except one, *Female Adjustment* and *Male Adjustment* were taken from the same study and were measured in the same units. The exception is the superb fairy wren, *Malurus cyaneus*, where *Female Adjustment* and *Male Adjustment* were calculated from different studies and were measured in different units.

Survival Rates and Body Mass

I collected data on adult survival rates and body mass (which strongly predicts variation in survival) from the literature for the 16 species for which I obtained an effect size (see above). In total, I obtained sex-specific survival and mass estimates for 15 of these species (supplementary Table 2).

Publication Bias Tests

To examine publication bias, I used Egger's regression method (Egger *et al.*, 1997; Moreno *et al.*, 2009) conducted in the MCMCglmm R package (Hadfield & Nakagawa, 2010; R Core Team, 2013) and trim and fill analyses conducted in the metafor R package. Egger's method: the precision with which main effects are estimated depends on sample size – we expect scatter when sample size are small and increasing precision as sample sizes increase. This gives rise to a 'funnel' shaped plot. If there is no relationship between effect size and sample size, we would expect a regression slope of zero. I regressed *Female Adjustment* and *Male Adjustment* against the inverse standard error of each effect size. I included study, species and a phylogenetic covariance matrix as random effects and weighted each effect size by the square of its sampling variance. For *Female Adjustment* there was a positive relationship between the size of the effect and the inverse of the standard error while for *Male Adjustment* there was no relationship between the size of the effect and the inverse of the standard error (*Female Adjustment*: slope (β) = 0.6, Credible Interval (CI) = 0.05 to 1.08, $N_{species}$ = 16, $N_{effect\ sizes}$ = 47; *Male Adjustment*: β = 0.11, CI = -0.39 to 0.64, $N_{species}$ = 16, $N_{effect\ sizes}$ = 47). Trim and fill analyses: my sample of female effect sizes would require four extra effect sizes to generate a symmetric funnel plot while my sample of male effect sizes requires none. These results suggest that *Female Adjustment* may be biased by sample size.

Phylogenetic Meta-analyses

First, I tested whether female and male breeders adjust their investment in parental care when helped. I constructed an intercept only multi-response model using the MCMCglmm R package. My response variables were *Female Adjustment* and *Male Adjustment* (both modeled using a Gaussian error distribution). Because some of the data points in these response variables are from the same study and there are multiple data points for some species and these species share evolutionary history, my response variables violate the statistical assumption of independence. To account for this non-independence between data-points, I included three random effects in my model. These take into account non-independence between data points arising due to repeated measures per study and per species as well as non-independence due to shared evolutionary history. I specified an unstructured variance–covariance matrix for *Female Adjustment* and *Male Adjustment* to estimate the correlation between these two variables, allowing me to test whether male and female breeders respond to helpers in the same way. I expect a positive correlation between *Female Adjustment* and *Male Adjustment* if the sexes reduce their investment in parental care by the same amount. I weighted each data point by the sampling error associated with each effect size to account for differences between studies in data quality.

Next, I tested for the predicted positive relationship between reductions in parental care and adult survival. For females I constructed a model with *Female Adjustment* as the response variable (modeled using a Gaussian error distribution) with female adult survival rate (arcsine and z transformed) as a fixed effect and I included female body mass (log and z transformed) as a covariate. I included the same three random effects in this model as described above to take into account non-independence between data points arising due to repeated measures per study and per species as well as non-independence due to shared evolutionary history. I weighted each data point by the sampling error associated with each effect size to account for differences between studies in data quality. I constructed an identical model for *Male Adjustment* with male adult survival rate and male body mass included as fixed effects.

I assessed model convergence by assessing plots of chain mixing and levels autocorrelation. To account for phylogenetic uncertainty in each of these models I repeated each one on 100 phylogenetic trees sampled at random from the posterior distribution of bird trees published by Jetz *et al.,* (2012). I combined the resulting posterior samples for parameter estimation. I report parameter estimates as the posterior mode (β) and credible interval (CI) of the combined posterior distributions of the Markov chain. Full details of burn-in, run length, priors as well as the model formula, including error structures, are reported in the supplementary R script.

RESULTS

Breeders reduce their investment in parental care when helped

Both female and male breeders significantly reduced their investment in parental care when helped across species (*Female Adjustment*: $\beta = -1.0$, CI = -1.5 to -0.47, $N_{species} = 16$, $N_{effect\ sizes} = 27$; *Male Adjustment*: $\beta = -0.84$, CI = -1.34 to -0.39, $N_{species} = 16$, $N_{effect\ sizes} = 27$; Figure 2). There was, however, considerable variation between species in the strength of this adjustment. Female breeders reduced their investment in parental care in 25 of the 27 effect sizes. In 12 of these the reduction in care was statistically significant. In only 2 of the effect sizes did female breeders increase their effort in parental care but in both, this increase was not statistically significant. The pattern was similar in male breeders. In 24 of the 27 effect sizes breeding males reduced their investment in parental care. In 9 of these the reduction in care was statistically significant. In the remaining 3 effect sizes male breeders appeared to increase their investment in parental care but, as with female breeders, this increase was not statistically significant.

Sex differences in adjustment

Female and male breeders appeared to adjust their investment in parental care differently when helped. The sexes rarely reduced their investment in parental care by a similar amount: in some cases females reduced their investment more than males while in other cases males reduced their investment more than females (Figure 3 – although the trend appears positive, these data points are not independent, which is accounted for by the random effects used in the estimation of the correlation coefficient below). Supporting this trend, the correlation between *Female Adjustment* and *Male Adjustment*, although positive, was not significantly different from zero ($\beta = 0.34$, CI = -0.43 to 0.72, $N_{species} = 16$, $N_{effect\ sizes} = 54$).

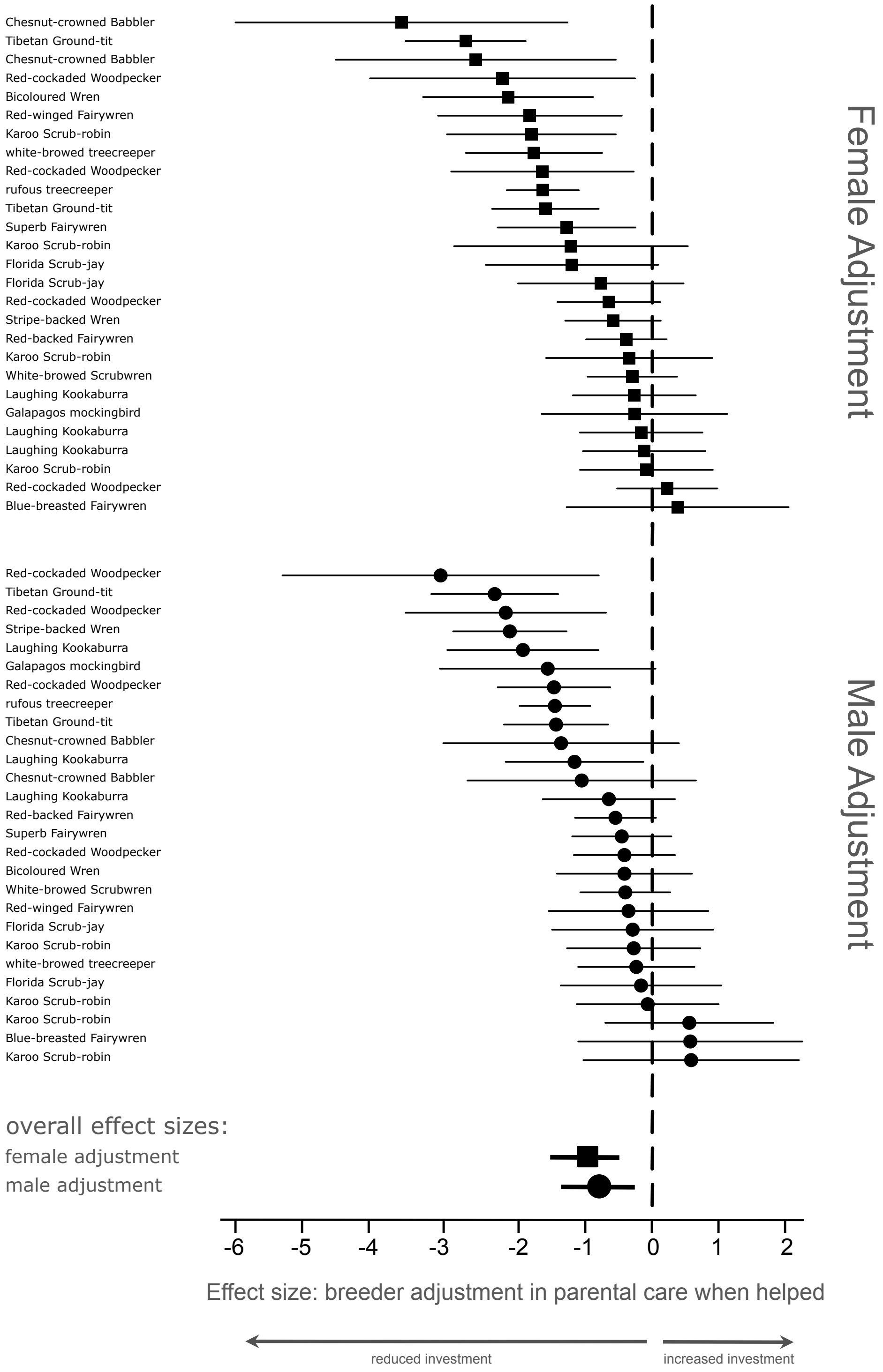


Figure 2. Female and male breeder adjustment in parental care when helped in facultative cooperatively breeding birds. Squares show *Female Adjustment* while circles show *Male Adjustment* and are bracketed by their 95% confidence intervals. The overall levels of adjustment across species for female and male breeders with the 95% credible intervals as estimated from the phylogenetic meta-analysis are shown below the individual effect sizes.

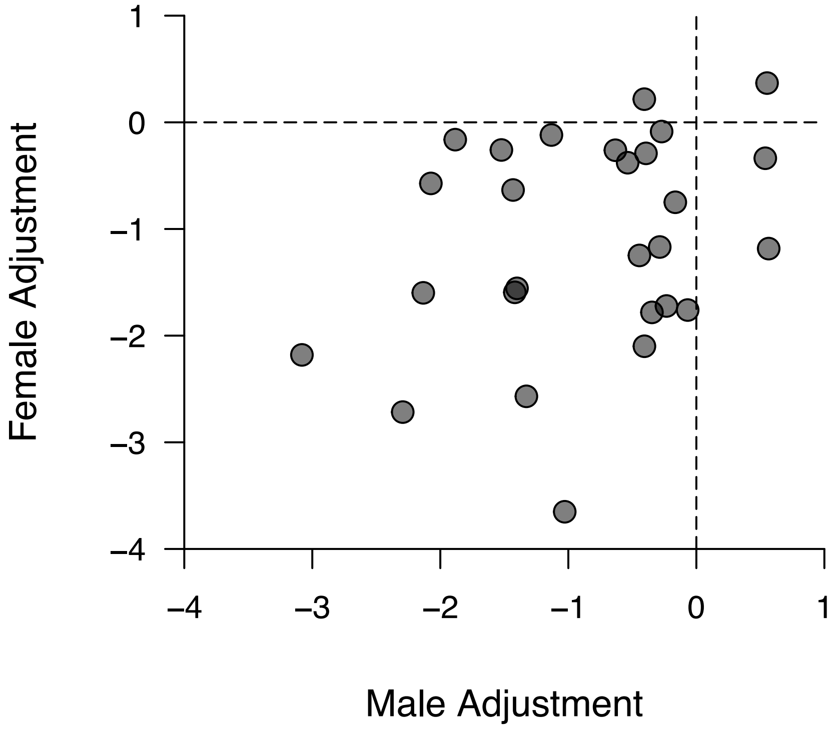


Figure 3. The correlation between *Female Adjustment* and *Male Adjustment*. A correlation of one would indicate that the sexes adjust their investment in parental care by an identical amount.

Breeders reduce their investment in parental care when survival is low

Female breeders appear to reduce their investment in parental care more when adult survival is low than when it is high, although this relationship is marginally non-significant (slope of *Female Adjustment* ~ female survival: β = 0.29, CI = -0.03 to 0.64, $N_{species}$ = 15, $N_{effect\ sizes}$ = 25). Similarly, male breeders reduce their investment in parental care more when adult survival is low than when it was high, although again, this relationship is marginally non-significant (slope of *Male Adjustment* ~ male survival: β = 0.32, CI = -0.09 to -0.76, $N_{species}$ = 15, $N_{effect\ sizes}$ = 25; Figure 4*b*).

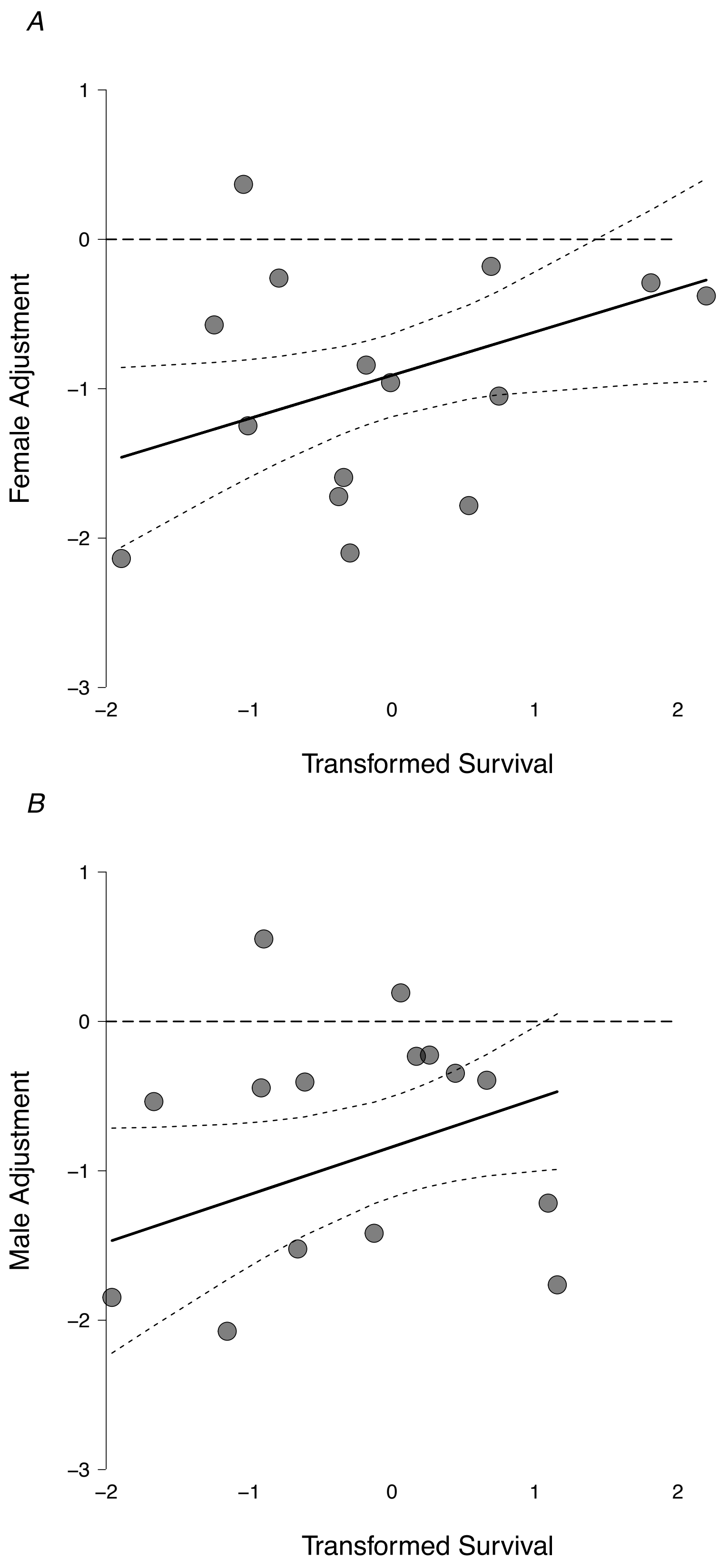


Figure 4. Female breeders (*a*) and male breeders (*b*) both reduce their investment in parental care more when adult survival is low than when it was high. Species averages are plotted with the regression line and 95% credible intervals.

DISCUSSION

Breeding individuals living in family groups reduce their investment in parental care when their offspring from previous broods help in raising young. This is a general trend across cooperatively breeding bird species. Between species there is considerable variation in the strength of this adjustment and breeding females and males appear to adjust their parental behaviour differently. The trend I detected between adjustment and survival is in the predicted direction for both female and male breeders. Both sexes reduce their investment in parental care more when survival is low and therefore by proxy the costs of care are high. This supports the prediction that breeders reduce their investment in offspring when the reproductive costs of care are high (Hatchwell, 1999; Hardling *et al.*, 2003; Johnstone, 2011).

I did not detect any complete reductions in parental care in cooperatively breeding birds. All breeders provided at least some care when they had helpers at the nest. The largest absolute reduction in parental care in my dataset occurred in the karoo scrub robin, *Erythropygia coryphaeus*, where females in pairs fed their offspring an average of 2.8 times per hour and reduced their feeding rate to just 0.6 times per hour in groups (Lloyd *et al.*, 2009). By comparing the adjustment in investment in parental care between pairs and groups and not taking into account how breeders respond to increasing group size, I may have been unable to detect a complete reduction in parental care by breeders. For instance, if breeders reduce their investment by a quarter for every helper at the nest, then once they have four helpers they will not provide any parental care.

I found considerable variability between the sexes in parental care. Breeding females and males rarely adjusted their parental behaviour by a similar amount when helped. For example, in the Galapagos mockingbird, *Mimus parvulus*, females did not adjust their investment in parental care but males did (Kinnaird & Grant, 1982) while in the bicoloured wren, *Campylorhynchus griseus*, the opposite was true (Austad & Rabenold, 1985). One explanation is that this is a sampling artifact resulting from a lack of statistical precision due to small sample sizes. However, theory predicts that the sexes may respond differently if the reproductive costs of care are sex specific (Johnstone, 2011). For example, differences in body size, incubation behaviour and colouration between the sexes could all result in higher costs of parental care for one sex.

In this study, I quantified how breeders in cooperatively breeding species adjust their investment in parental care in response being assisted in offspring care by nonbreeding helpers. My results show that across species, breeders consistently reduce their investment in parental care when helped. I found that the amount that breeders adjust their care is highly variable between species and between the sexes within a species.

Chapter 7

Discussion

Each of the previous chapters contains its own extensive discussion. This chapter therefore discusses general results and common themes of this thesis.

Family Matters

Recent work has argued that cooperative breeding in family and in non-family groups are variants of the same breeding strategy and that their origins should be explained by a common set of factors (Cockburn, 2013; Dillard & Westneat, 2016). However, kin selection will only operate in groups of relatives and therefore different selection pressures should favour cooperation in family and non-family groups (Hamilton, 1964a; b; Gardner et al., 2011; Bourke, 2011). In family groups, we expect females to be monogamous to ensure high relatedness between helpers and offspring whereas in non-family groups we expect high rates of polyandry to ensure all breeders gain an equal share of reproduction. In chapter 5 I used ancestral state reconstructions to test this prediction (manuscript in preparation). Across birds, cooperative breeding in family groups evolved from relatively monogamous ancestors. In non-family groups, however, levels of ancestral polyandry did not influence the likelihood of cooperative breeding evolving: the ancestors of species that breed cooperatively in non-family groups are as polyandrous as the ancestors of non-cooperative species.

Differences in relatedness between group members should also explain variation in social complexity in cooperatively breeding birds. Helping will only be altruistic if groups consist of related individuals. In non-family groups helping will be mutually beneficial. I tested this prediction in chapter 5 and found that there is a reproductive division of labour in family groups (helpers do not reproduce) and group sizes are typically larger than they are in non-family groups where group members are co-breeders. Similar trends have been observed in other clades. For example, in the social hymenoptera, eusociality has only evolved from monogamous ancestors living in family groups (Hughes et al., 2008) and transitions to obligate multicellularity from single-celled organisms have only happened in clonal groups (Fisher et al., 2013).

Direct Fitness is Important, Even in Family Groups

Inheriting a breeding position in many cooperatively breeding species leads to considerable direct fitness gains. For example, in the naked mole-rat, *Heterocephalus glaber*, breeding females may produce over 900 pups in their lifetimes (Buffenstein, 2008). Long life ensures a long breeding tenure once a breeding position is inherited and is therefore predicted to be an important driver of the transition to cooperative breeding[3] (Pen & Weissing, 2000; Wild & Koykka, 2014). In chapter 3 I found support for this prediction by showing that the ancestors of cooperatively breeding birds are longer-lived than the ancestors of non-cooperative species (published in *Proc. B*). Importantly, queuing to inherit the nest is not a strategy used by helpers for obtaining direct fitness – breeders monopolise reproduction.

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[3] This prediction only applies to family cooperative breeders. Lifespan is unlikely to influence the transition to non-family cooperative breeding in the same way since group members are co-breeders and there is no breeding position to inherit. Unpublished data suggest that non-family cooperative breeders have significantly lower levels of annual survival than family cooperative breeders.

Nest inheritance is thought to have been an important driver of the transition to cooperative breeding in other clades. For example, the prototermite is likely to have been a long-lived cooperative breeder in which nest inheritance favoured cooperation (Bignell *et al.*, 2010). Similarly, in the paper wasp, *Polistes dominulus*, females that inherit a nest have higher fitness than females that breed independently, providing a strong incentive for cooperation (Leadbeater *et al.*, 2011). Even in ants, helpers can inherit breeding positions. This is the case in the 'primitive' ants, *Nothomyrmecia macrops* and *Dinoponera quadriceps* in which there is weak dimorphism between reproductive and non-reproductive females (Monnin & Peeters, 1999; Sanetra & Crozier, 2002). It is not clear whether nest inheritance currently plays a role in maintaining helping behaviour, albeit as a secondarily derived elaboration.

How Much to Help is Shaped by Opportunities for Direct Fitness

One way to explore the role of direct fitness in family groups is by controlling for variation in relatedness. Any remaining variation in cooperative behaviour should therefore reflect differences in strategies to maximise direct fitness. In chapter 4 I used this logic to demonstrate that sex-biased dispersal shapes investment in helping behaviour (in review at the *American Naturalist*). The sex that has a higher probability of breeding in its natal group helps more than the dispersing sex. The tendency for the philopatric sex to help more than the dispersing sex is also observed in cooperatively breeding mammals. For example, in cotton-top tamarins, *Saguinus oedipus*, males are philopatric and male helpers care more for infants than female helpers (Zahed *et al.*, 2010). In meerkats, *Suricata suricatta*, females are philopatric and female helpers contribute more to babysitting and pup feeding than male helpers (Clutton-Brock *et al.*, 2002).

A high probability of inheriting a breeding position is not always associated with increased investment in helping behaviour. In *P. dominulus*, females next in line to inherit a breeding position work less hard than other females in their social group (Cant & Field, 2001). One reason for this difference could be that mortality rates are substantially higher in this species than they are in birds or mammals, and therefore increased help leads to a decreased probability of inheriting a breeding position. This exception demonstrates that although future direct fitness shapes investment in cooperative behaviour, the direction of this investment will depend on life history and demographic parameters. I would like to extend my work by testing how lifespan influences whether helpers increase or reduce their investment in care in response to future breeding opportunities by incorporating data from across taxonomic groups including insects, mammals and fish.

The End of Direct Fitness

In chapter 2, I argued that the transformation of cooperatively breeding groups into societies with sterile helpers requires completely overlapping generations in addition to lifetime genetic monogamy (published in *BioEssays*). In this way, helpers can do as well by helping as they can by breeding for their entire lifespans. Consistent with this prediction, breeders are exceptionally long-lived while worker lifespans are considerably shorter in many eusocial societies. Breeding individuals in eusocial societies are also exceptionally fecund. For example, queens of the termite, *Macrotermes subhyalinus*, have swollen abdomens which hold enlarged ovaries allowing them to lay up to 40 000 eggs per day (Wyss-Huber & Luscher, 1975). This reversal of the longevity/fecundity trade-off remains a poorly understood aspect of insect sociobiology (Helantera, 2016; Séguret *et al.*, 2016).

A likely step in the reversal of the longevity/fecundity trade-off is for breeders to invest more of their resources into fecundity and survival and less in parental care. This trend is evident in cooperatively breeding birds, as demonstrated in chapter 6. Both male and female breeders significantly reduce their investment in parental care when helped. Exploring whether this reduction in care is associated with increased breeder survival and fecundity could provide insight into the origins of the reversal of the longevity/fecundity trade-off.

Concluding Remarks and Future Directions

There are clear differences in many aspects of the biology of vertebrates, invertebrates and microorganisms. Despite these details, a set of common principles underlying the evolution of cooperative behaviour across taxa is beginning to emerge. This extends beyond relatedness, as I have demonstrated in this thesis. Lifespan provides a clear example of a life-history trait that influences the direct fitness benefits of cooperating, and sex-biased dispersal is an example of a demographic parameter that determines investment in cooperative behaviour.

Cooperatively breeding birds have so far provided a valuable resource for testing inclusive fitness theory. Further comparative studies on birds are likely to reveal new patterns that need explaining. Extending the comparative approach to studying social evolution in other clades is, however, essential for confirming that a set of common principles does indeed underlie the evolution of cooperative behaviour. This will be possible as more studies are published on organisms across the domains of life and as our knowledge of the phylogenetic relationships among these species improves.

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Appendices

- A – Farine, D. R, Downing, C. P. & Downing, P. A. (2014). Mixed-species associations can arise without heterospecific attraction. *Behavioral Ecology*, 25: 574-581.
- B – Cornwallis, C. K., Botero, C. A., Rubenstein, D. R., Downing, P. A., West, S. A. & Griffin, A. S. (accepted). Cooperation facilitates the colonisation of harsh environments. *Nature Ecology and Evolution*.

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Original Article

Mixed-species associations can arise without heterospecific attraction

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Despite widespread research on the interaction rules that drive group-living behavior in animals, little is known about the spatial self-organization of individuals in heterospecific groups. This has led to significant challenges in teasing apart the various mechanisms thought to underpin multispecies groups. One potentially useful approach for gaining an understanding of this process is to identify the rules that best predict the observed distribution of individuals across these groups. In order to gain an insight into the decision-making process that might generate patterns of heterospecific associations, we collected data on the number and distribution of nests in breeding colonies that contained 3 species of weaverbird. We found no evidence of segregation by species, either within or between colonies. Using agent-based simulations of males applying different rules of attraction and repulsion to conspecifics or heterospecifics, we found that the best-fitting rule contained no heterospecific attraction. In this rule, individuals picked colonies based on an optimal distribution of conspecific nests. Given that nests are an important sexual signal in weavers, our findings suggest that this rule is biologically relevant: Males are seeking an optimal trade-off between attracting females via lekking and competing for mates if too many conspecific nests are present.

Key words: **collective animal behavior, colonial breeding, competition, interspecific interactions, Ploceidae, self-organization.**

INTRODUCTION

Associations between heterospecifics are generally considered to arise when participants gain shared benefits of living in groups at a reduced cost of competition (Alexander 1974; Krause and Ruxton 2002). Benefits such as reducing predation risk (Krause and Ruxton 2002; Harrison and Whitehouse 2011), finding food (Aplin et al. 2012), or increasing foraging efficiency (Sridhar et al. 2009) may be attained by maintaining cohesion (Conradt and Roper 2000). Morse (1970) incorporates this assumption into his classic definition: “[group] formation depends upon the positive responses by individuals to members of their own or other species.” However, the rules that individuals apply to conspecifics and heterospecifics when making grouping decisions are rarely quantified. Thus, teasing apart competing mechanisms has remained challenging in this area (Sridhar et al. 2009).

Studies on fish provide the best evidence of how fundamentally different mechanisms can drive mixed-species grouping. For example, small juvenile fish of different species might fill closer niches or be physiologically more similar than conspecifics of different ages (Hoare, Krause, et al. 2000; Ward et al. 2002). Assortment with heterospecifics by body size can then provide shared antipredator benefits (such as through the oddity-effect; Landeau and Terborgh 1986). However, this pattern can also emerge simply through differences in habitat use by differently sized individuals (Hoare, Ruxton, et al. 2000; Croft et al. 2003; Jones et al. 2010). Thus, the functional cause of heterospecific associations can be either physical or social through active choice.

However, there have been fewer studies that have investigated the role of conspecific interactions in mixed-species associations. Buskirk (1976) suggests that intraspecific competition plays a primary role in the shift from monospecific to heterospecific groups, but only if predation risk is high (see also Beauchamp 2004). One frequent pattern that emerges in studies of mixed-species flocking is the attraction of “peripheral” species to “nucleus” species that are typically highly vigilant and provide foraging benefits by reducing vigilance (Sridhar et al. 2009, 2013). In contrast, other studies have found a strong link between niche overlap (or phenotypic similarity) and association strength, both at a species (Sridhar et al. 2012) and individual level (Farine and Milburn 2013). Within-species variation may also be prominent, for example dominance interactions may play an important role in predicting association patterns, with subdominants driven out of conspecific groups (Farine et al. 2012).

Colonial breeding, which is thought to confer similar benefits to group foraging (Brown and Brown 2001) such as added protection

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from predators (Pius and Leberg 1998; Lima 2009), may be a good place to investigate the behavioral rules driving heterospecific associations. Single colonies that contain multiple species each represent a single discrete choice by individuals, providing an opportunity to explore decision making in the context of group choice. For example, weaverbirds (family Ploceidae) regularly nest in large colonies that often comprise a mixture of conspecifics and heterospecifics (Collias and Collias 1964; Crook 1964; Din 1991, 1992; Lahti et al. 2002; del Hoyo et al. 2010). In several species, the polygynous males are strongly territorial within their colony, building several nests as a sexual signal to attract females (Collias and Collias 1964; Crook 1964; Din 1992; del Hoyo et al. 2010). Given the importance of nests for male fitness and the regular occurrence of mixed-species colonies, weavers provide a useful system in which to investigate the rules underlying conspecific and heterospecific associations.

In this study, we use data on the distribution of nests across a number of neighboring mixed-species weaverbird colonies to determine the interaction rules that drive the pattern of species associations across a savannah landscape. We measured the location of nests within multiple colonies to test if species were spatially segregated both across the landscape and within trees. We then quantified a number of possible interaction rules into predictive models, confronting these with the empirical data in order to determine which rules best predicted the patterns we observed. Rules forming hypotheses for explaining individual colony choice were formulated based on different combinations of 4 simple parameters: 1) attraction to conspecifics, suggesting that colonial breeding provides social benefits such as attracting mates or diluting predation risk; 2) repulsion from conspecifics, which would suggest that colonial breeding is driven by resource limitation (such as the number of available sites); 3) attraction to heterospecifics, which would suggest a role of predator dilution driving colonial breeding (large colonies are beneficial), but that these introduce other components of intraspecific competition; and 4) avoidance of heterospecifics, which would suggest that there are limited benefits associated with large colony sizes, such as predator dilution. Fitting simulated data to the empirical data enabled us to gain insight into the biological mechanisms that may be driving mixed-species colonial breeding in these species.

METHODS

Study site

This study was carried out on the Kisenyi plains, Queen Elizabeth National Park, Uganda (0.3833° S, 29.9667° E), in July 2012. This period falls within the rainy season, during which weaver breeding is synchronized. Suitable areas for the study within the park were selected by preliminary observations with fifteen 10 × 10 km suitable plots being identified. The final site was chosen at random using the "sample" function in R (R Development Core Team 2013). We restricted our study to the open savannah in order reduce the potential for confounding effects, such as attraction to water (some weaver species specialize by nesting over water), that may generate colony structure as a by-product of nesting niche specializations. The dominant species of tree in the study plot was *Acacia xanthophloea*, the fever tree.

Field observations

The colonies within the study area were mapped using Global Positioning System. The height of each tree was measured using a Suunto Optical Height Meter PM-5/1520. For each tree, we counted the number of nests of each species using the Crook (1963) classification of nest types and the morphological divergences between the weaver species present. To ensure accuracy, counts were repeated 3 times by the same observer (C.P.D.). We also recorded the heights of the first and last nest of each species nest occurrence in each tree (defining this distance as the nesting potential).

Data analysis

We first assessed whether species were spatially disaggregated. Two measures here were appropriate: spatial segregation between colonies and spatial segregation within colonies. To assess the former, we mapped the distribution and composition of each colony. To assess the latter, whether species nest at different heights in which case each species' colony would be determined by independent joining rules, we compared the distances of nests from the lower and upper nesting limits for each species. We then tested if the total number of nests was dependent on the nesting potential (the total available space in which to build nests, defined as the distance from the lowest to the highest nest in each tree). This was a good predictor for tree height and tree width (height and nesting potential, $r = 0.58$; width and nesting potential, $r = 0.42$). Because the total number of nests per tree is count data, we used a Generalized Linear Model with aQuasi-Poisson error distribution (because in all cases, the dispersion parameter was >1, Crawley 2007).

We then tested whether conspecific or heterospecific aggregations were spatially assorted or disassorted using the network assortativity coefficient (Newman 2002). We constructed a network of colonies (using the R package asnipe; Farine 2013), defining each dyadic edge weight as the inverse of the distance between a pair of colonies (forming a full-connected network), and used the "assortnet" package (Farine 2014) in order to calculate the weighted-network assortativity coefficient and the standard error. This measure, based on Pearson's correlation coefficient, ranges from 1 for positive assortment (which would suggest that colonies were more alike if they were closer in space) to −1 for disassortment (which would suggest neighboring colonies are more unlike each other than expected by chance). We defined each colony as ranging from entirely conspecific to evenly mixed using Shannon's diversity index (Shannon 1948). In addition, we tested whether overall colony size and nesting potential was random using the same method.

In order to gain insight into what processes could lead to the observed distribution of nests across colonies, we developed computer simulations comprising 12 decision rules. First, we tested a null model, in which male weavers randomly chose a colony irrespective of the distribution of conspecifics or heterospecifics. The next 4 rules were made up of single parameters representing attraction or repulsion from conspecifics or heterospecifics; for example rule (ii) males were attracted to trees above a minimum number of conspecific nests ("attraction to conspecifics only"). Rules (xi)–(ix) contained 2 parameters, for example rule (ix) males avoided trees above a threshold number of nests ("repulsion from conspecifics and heterospecifics"). Rules (x) and (xi) contained conspecific attraction and repulsion, combined with a third parameter of either attraction or repulsion from heterospecifics, for example rule (x) males were attracted to trees above a minimum number of conspecific nests, but below a maximum number of conspecific nests ("attraction and repulsion from conspecifics"), and attracted to large colonies ("attraction to heterospecifics"). Finally, we tested a rule with all 4 parameters combined, which would suggest that male weavers had an optimum colony size, both in terms of intraspecific competition, but also for overall dilution of predation risk. For these rules, we define the probability of choosing a particular tree as a single-parameter sigmoidal function defined as:

$$P(X)=\frac{1}{1+2^{-(\tau_r-n_x)}}$$

for repulsion rules, and:

$$P(X)=\frac{1}{1+2^{-(n_x-\tau_a)}}$$

for attraction rules, where $P(X)$ is the probability of choosing tree X, n_x is the number of relevant nests on tree X, τ_r is the upper (for repulsion) and τ_a is the lower (for attraction) threshold value, which can range from 0 to the maximum colony size. These sigmoidal curves operate as step functions, though always have a small probability that wrong decisions can be made (trees never have an absolute probability of 0 or 1, unless there is only one choice). For decision rules incorporating more than one of the above functions, the total sum of $P(X)$ for all trees is used to scale the total probability of picking a tree to always equal 1 (probability matching). For example, for each tree X in rule (xii), we summed the 4 probabilities (conspecific attraction, conspecific repulsion, heterospecific attraction, and heterospecific repulsion) for each tree and divided this by the sum of the 4 probabilities for all trees.

We calculated the Shannon's diversity index (Shannon 1948) of each tree (in both the observed and simulated data) and used maximum likelihood estimation to estimate the best-fitting value of τ for each rule. For each possible parameter value (or combination of parameter values), we allocated each nesting male using the rules of attraction and repulsion in order to calculate the probability of picking a given tree (see below). For each parameter value (or combination of parameter values), we calculated the log-likelihood of our observed data using the distribution of results from 1000 simulations. The parameter values with the highest log-likelihood value represented the best fit to our data. We then compared the fit of each rule by calculating the Akaike Information Criterion (AIC) value from the log-likelihood of the best-fitting parameter set.

Finally, in order to assess how well each rule re-created the biological pattern, we used the *lm* function to fit a logarithmic curve to the observed and simulated data points. We used the "predict" function to generate 95% confidence intervals of the observed logarithmic relationship. All analyses were conducted in R version 3.0.0 (R Development Core Team 2013).

Simulations

Simulations were run as follows: 1) we created a list of all individual nests (maintaining the distribution by species we observed) and a list of empty trees (where each tree had the observed number of available spaces); 2) we randomly picked a nest from the available pool, using the current rule to calculate the probability of choosing each of the trees with space remaining; and 3) we randomly sampled a tree, using the given probabilities of drawing each tree, allocating that nest to the tree and removing the availability of sites on that tree by one. We repeated these steps until every nest was allocated to a tree and repeated the simulations 1000 times for each rule in order to generate a mean and 95% confidence range of the diversity index score for each tree. Overall colony sizes were kept constant for all simulations as previous studies suggest that these are consistent across years (Spottiswoode 2007). Although this may give qualitatively different results to a simulation allowing colony size to vary, we found no strong predictors, such as nesting potential, which we could use to model new colony sizes.

RESULTS

In total, among savannah *A. xanthophloea*, 14 trees were identified that contained colonies. This represented the northwest corner of the study area that was largely dominated by water in the south-eastern section (see Supplementary Google Earth KMZ file). These colonies contained the nests of 3 species of *Ploceus* weaver: yellow-backed (*Ploceus melanocephalus*), black-headed or village (*Ploceus cucullatus*), and lesser masked (*Ploceus intermedius*) (see Figure 1). We counted a total of 2261 nests, of which 770 (34%) were of lesser masked, 1063 (47%) of black-headed, and 428 (19%) of yellow-backed weavers. These data and associated spatial position of nests are presented in Table 1.

Spatial variation within and between trees

We found no qualitative differences in the spatial distributions of species across the study site (Figure 1) or in the distribution of species within colonies (Figure 2). Most colonies were found in nearby trees close to at least one other. Trees were not evenly distributed in this landscape, and all patches, except for a single isolated colony, contained nests of at least 2 species and most colonies contained nests of all 3 species (Table 1).

The degree of interspecific mixing in each colony was also random with respect to space. Using the network assortativity coefficient, we found no relationship between the Shannon Index and the distance between trees (r = 0.019 ± 0.139). However, we did find a correlation of colony size and proximity (r = 0.232 ± 0.082). Although this could suggest some social enhancement as we found no evidence of spatial similarity in nesting potential (r = −0.077 ± 0.195), the pattern was probably driven by 3 of the 4 smallest colonies being found together (see Figure 1).

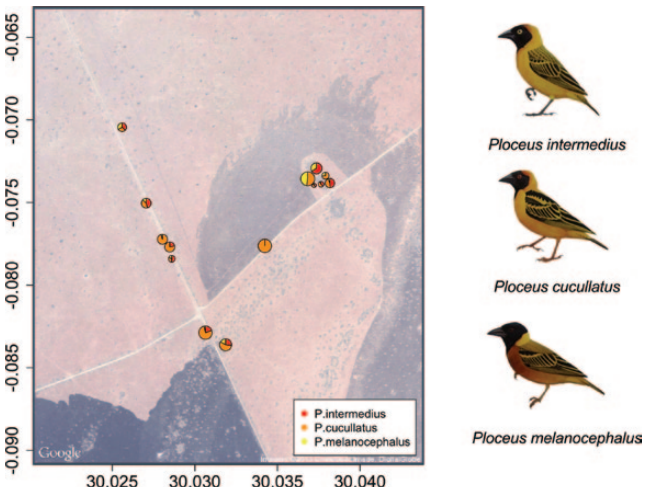

Figure 1
Distribution of colonies within the study area and proportion of nests by species in each tree. The size of each pie chart represents the height of the tree. The map is a total of 1.3 km east–west and 1.4 km north–south. Weaver plates from del Hoyo et al. (2010).

Table 1

Summary of the counts and distribution of species nests for each tree sampled in the study area

	Ploceus intermedius		*Ploceus cucullatus*		*Ploceus melanocephalus*			
Tree ID	Nests	Height (m)[a]	Nests	Height (m)[a]	Nests	Height (m)[a]	Total	NP (m)[b]
1	291	1.5–10	226	10.0–12.0	257	10.0–12.0	774	10.5
2	144	2.0–12.5	125	12.5–13.5	43	12.5–13.5	312	11.5
3	0	—	146	3.0–7.0	8	7.0–14.0	154	11
4	39	4.0–5.5	142	1.5–8.5	0	—	181	7
5	49	5.5–5.5	29	5.5–9.0	18	5.5–9.0	96	3.5
6	0	—	10	10.5–12.5	0	—	10	2
7	37	3.5–16.5	0	—	19	4.0–16.5	56	13
8	0	—	12	10.5–19.5	11	10.5–19.9	23	9
9	34	4.0–5.0	39	4.0–5.0	8	4.0–5.0	81	1
10	0	—	67	2.5–9.5	25	2.5–9.5	92	7
11	68	7.5–11	64	7.5–11.0	8	7.5–11.0	140	3.5
12	73	2.5–8.0	103	3.0–7.0	15	3.0–7.0	191	4.5
13	13	6.5–7.0	52	7.5–19	2	7.5–19.0	67	12.5
14	22	4.0–17.0	48	6.0–17.0	14	6.0–17.0	84	13

Each row is a different tree.

[a] Nesting heights are given as lowest nest to highest nest for each given species.

[b] NP is the nesting potential, or total range of nests from all species.

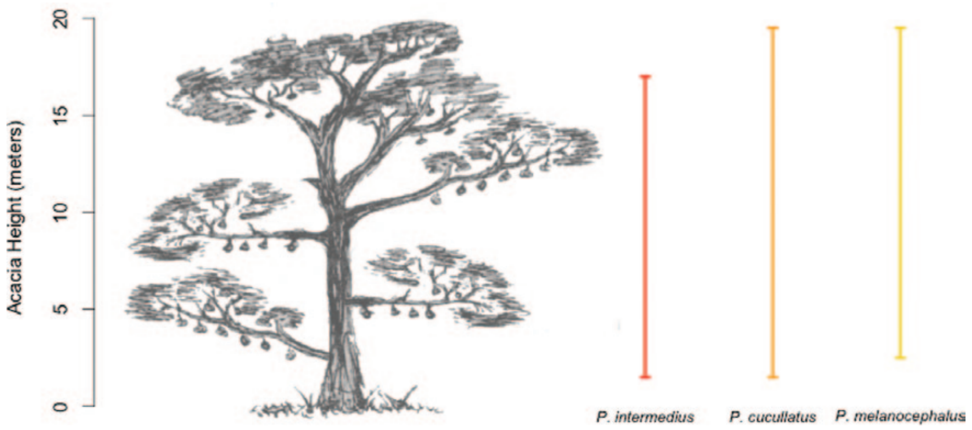

Figure 2

There was no clear distinction in nesting height between species. We measured the minimum and maximum nesting heights for each species across all colonies in which they were observed and found that these mostly overlapped. Hence, within-colony segregation by species is unlikely to explain our results.

Relationship between nesting potential and colony size

The total number of nests per tree was not related to nesting potential ($t = 0.826$, df = 13, $P = 0.425$; Figure 3). This shows that trees with greater nesting potential do not simply contain more nests and implies a limit to colony size. This is important because if trees with greater nesting potential had more colonies, then the observed number of species per tree could simply be related to nesting potential, with larger trees more likely to contain more nests of each species simply by chance.

Rules of attraction and repulsion

We found a good fit of a logarithmic increase in diversity in larger colonies (Figure 4a). By simulating data using each rule (Table 2), we found that a rule that combined attraction to conspecifics but avoidance of large colonies of conspecifics best replicated the data (rule vi, Figures 4b, 5, and 6). This rule generated the same patterns of large variation for small colony sizes (which range from being entirely monospecific up to a diversity index of almost 1, Figure 4b), whereas larger colonies had consistently high values of species diversity. In contrast, repulsion from conspecifics (rule iii), repulsion from heterospecifics (rule v), attraction to large colonies (rule viii), or repulsion from large colonies (rule ix) had almost identical outcomes and all resembled the null model (rule i, Figures 4c and 6). Attraction to heterospecifics (rule iv), an optimal rule of attraction and repulsion from heterospecifics (rule vii), heterospecific attraction with the optimal conspecific rule (rule x), and the combination of attraction and repulsion for the entire set of nests (rule xii) all resulted in an underestimate of colony diversity. Finally, a rule of simple attraction to conspecifics (rule ii) and the optimal attraction-repulsion rule for conspecifics combined with heterospecific repulsion (rule xi) were also strongly supported by AIC (Table 2). The 3 best-fitting models all contained attraction to conspecifics, whereas repulsion from conspecifics was present in the 2 top models. There is evidence that heterospecific repulsion may also contribute to the observed distribution of nests across colonies, potentially as male weavers preferentially avoid large

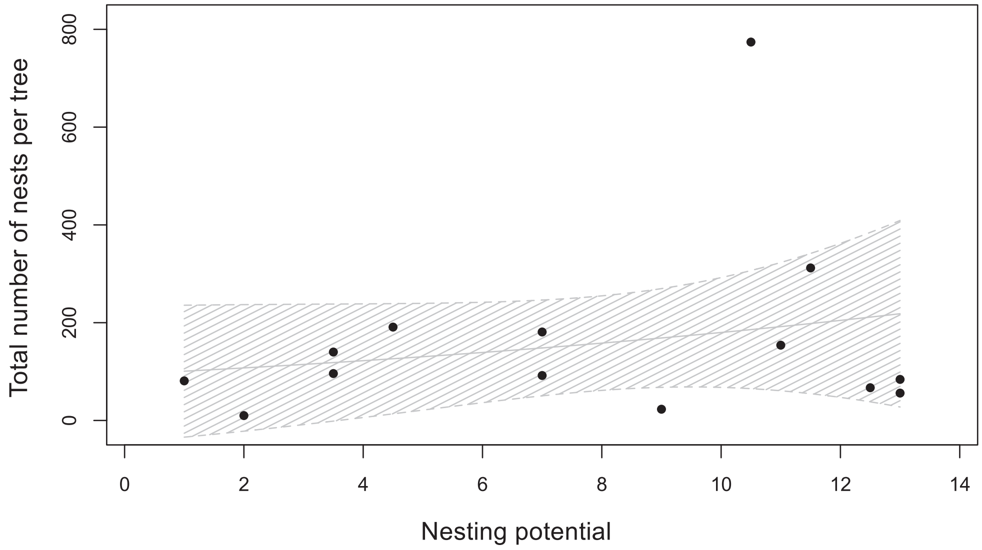

Figure 3

There was no relationship between the total number of nests per colony and the nesting potential (linear model estimate ± standard error = 0.004 ± 0.006, t = 0.784, df = 12, P = 0.44). Each filled circle represents one breeding colony. Nesting potential was measured as the distance from the lowest to the highest nest in each tree. The shaded region represents the 95% confidence interval as predicted by the linear model.

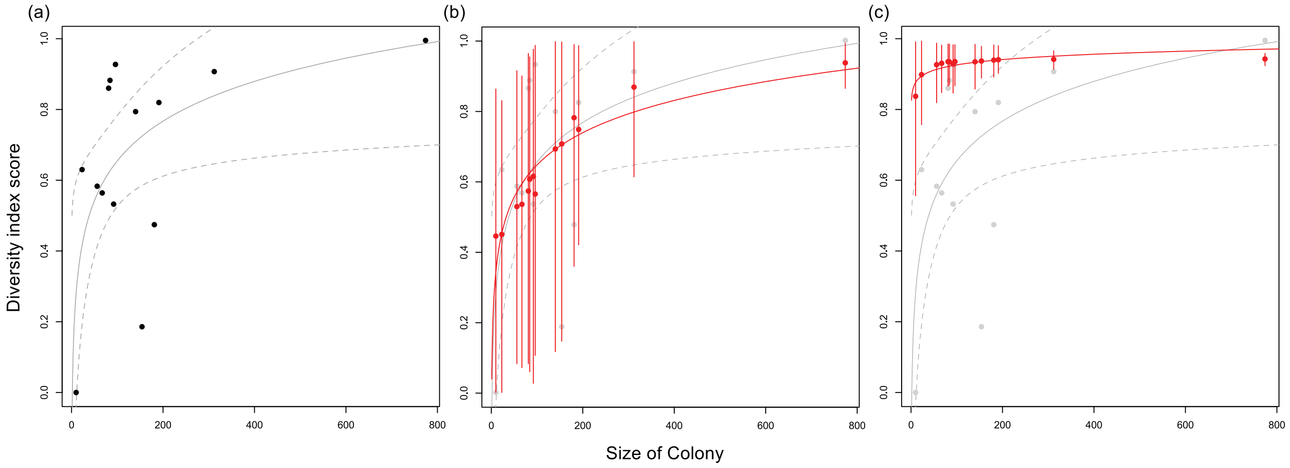

Figure 4

The observed logarithmic relationship between species diversity and colony size (grey curve with 95% confidence interval, log intercept = −0.092, coefficient ± standard error = 0.16 ± 0.06, P = 0.02) (a) was replicated well by rule (vi) consisting of attraction to conspecifics but repulsion from large colonies of conspecifics (b; attraction τ = 6 nests, repulsion τ = 158 nests; see Figures 5 and 6 and Table 2). In comparison, a null model of random colony choice (c), rule (i), consistently resulted in small colonies that were too diverse, with too little variance. Red lines represents model fit to the simulated points, red bars indicate indicate the 95% range of the diversity index for each nest from 1000 simulations, and the red points are the means of the simulations for each colony. Solid gray lines are the model fit of the observed data (from a), dashed grey lines are the 95% confidence intervals of the model fit from the observed data, and grey points are the observed diversity values for each colony.

colonies. We found no support for any rule containing heterospecific attraction.

DISCUSSION

We have shown that the distribution of species in mixed colonies can be realistically replicated using a simple decision rule: nest with conspecifics, but not too many. Importantly, this rule does not require a heterospecific attraction parameter, suggesting that, at least in this system, mixed-species associations can arise as a by-product of within-species self-organization. This makes sense in light of previous studies which found that the nest is an important signal of male quality in courtship (Collias and Collias 1959; Collias and Victoria 1978; Jacobs et al. 1978) and suggests that individuals may be optimizing colony size as a trade-off between attracting females and competing with males of their own species for mating opportunities.

Male weaverbirds may be strongly motivated to avoid conspecifics due to intrasexual competition for mates. Individual males may typically build several nests in a season or even have multiple nests within their territories at any given time (Collias and Collias 1964). This is a significant investment, given that a nest can take between 9 h to 2 days to build and require an average of 30 km of flight (Collias and Collias 1967; Din 1992). Furthermore, if a female does

Table 2
Summary of all the rules that were tested on the observed data

		Conspecifics		Heterospecifics			
Rule	Results	τ_a	τ_r	τ_a	τ_r	AIC	ΔAIC
i	Random	—	—	—	—	3589.0	3572.53
ii	C attraction	6	—	—	—	20.42	3.95
iii	C repulsion	—	158	—	—	1754.11	1737.64
iv	H attraction	—	—	66	—	2156.92	2140.45
v	H repulsion	—	—	—	186	2553.27	2536.80
vi	**C attraction and C repulsion**	**6**	**158**	—	—	**16.47**	**0.00**
vii	H attraction and H repulsion	—	—	16	140	70.83	54.36
viii	C attraction and H attraction	9	—	16	—	2019.38	2002.91
ix	C repulsion and H repulsion	—	58	—	140	2036.65	2020.18
x	C attraction, C repulsion and H attraction	8	170	21	—	50.00	33.53
xi	C attraction, C repulsion and H repulsion	6	92	—	197	16.52	0.05
xii	C attraction, C repulsion, H attraction, H repulsion	7	170	24	140	36.06	19.59

The model in bold is the most supported. The best-fitting values of attraction (τ_a) and repulsion (τ_b) for conspecifics and heterospecifics in each model were inferred using maximum likelihood estimation. AIC and ΔAIC were calculated from the log-likelihood of each model. The best supported model (vi) is shown in bold. Conspecific and heterospecific are abbreviated as C and H, respectively.

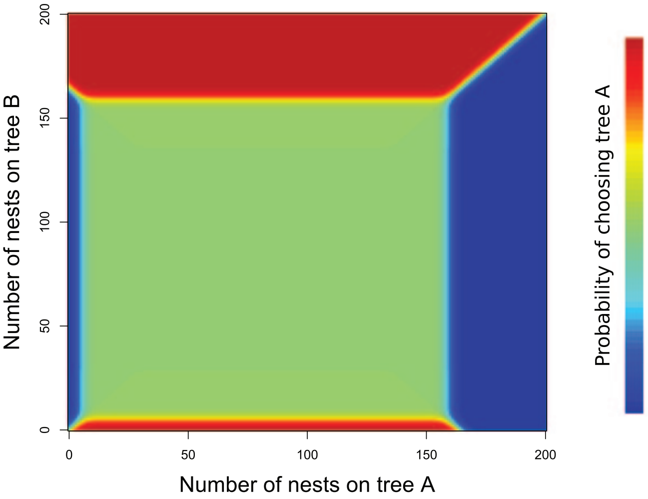

Figure 5
The best-fitting rule predicts that given a choice between 2 trees, male weavers almost always picked tree A if the number of conspecific nests on tree A was greater than 6 but less than 6 on tree B. If the number of conspecific nests on both trees was greater than 6 but less than 158, then they had an equal probability of picking either tree, regardless of the number of nests they contained within that range. If the number of nests on tree A was greater than 158, but on tree B was less than 158, then the bird would pick tree B. Finally, if both trees had large colonies of conspecifics, the bird generally picked the tree with the smallest colony.

not accept a nest within a given interval, a male may tear it down and build a new one (Collias and Victoria 1978). Conspecific competition may further reduce the chances of any single male mating successfully both through a simple dilution effect and by increasing the chances that a “higher quality” competitor will be within a male’s vicinity (Brown and Brown 2001). A male should therefore behave so as to minimize these energetic demands, and our rule suggests that, in these species, males avoided large colonies containing numerous nests.

One way that males may be able to avoid these costs but still maintain putative benefits such as avoiding predation is to nest among heterospecifics. However, given the importance of attracting mates, we suggest that this strategy may not be beneficial as it could result in the male being “invisible” to females of his own species. For instance, a tree in which the predominant displaying species is black would differ greatly in appearance from one in which the birds performing their display are yellow (Crook 1963). Thus, despite the costs associated with intraspecific competition, males should be attracted to conspecifics. An important reason for this is that larger colonies are more successful in attracting females (Collias and Collias 1969). Intuitively, the savannah habitat these species of weaver inhabit is open and widely spaced, therefore females are more likely to notice larger colonies. Furthermore, from a female’s perspective, visiting the largest colony could provide the best opportunity for comparing male quality, thus colonies could potentially also be operating as a form of lek. We found that a rule which avoided colonies with no conspecifics provided the best fit to our observed data, highlighting a strong tendency to join existing colonies of conspecifics.

A further consideration is that colonies in and of themselves should be at an optimal size (Brown et al. 1990). This involves balancing benefits, such as reduced risk of predation, with the costs of increased competition for resources and elevated risk of attracting

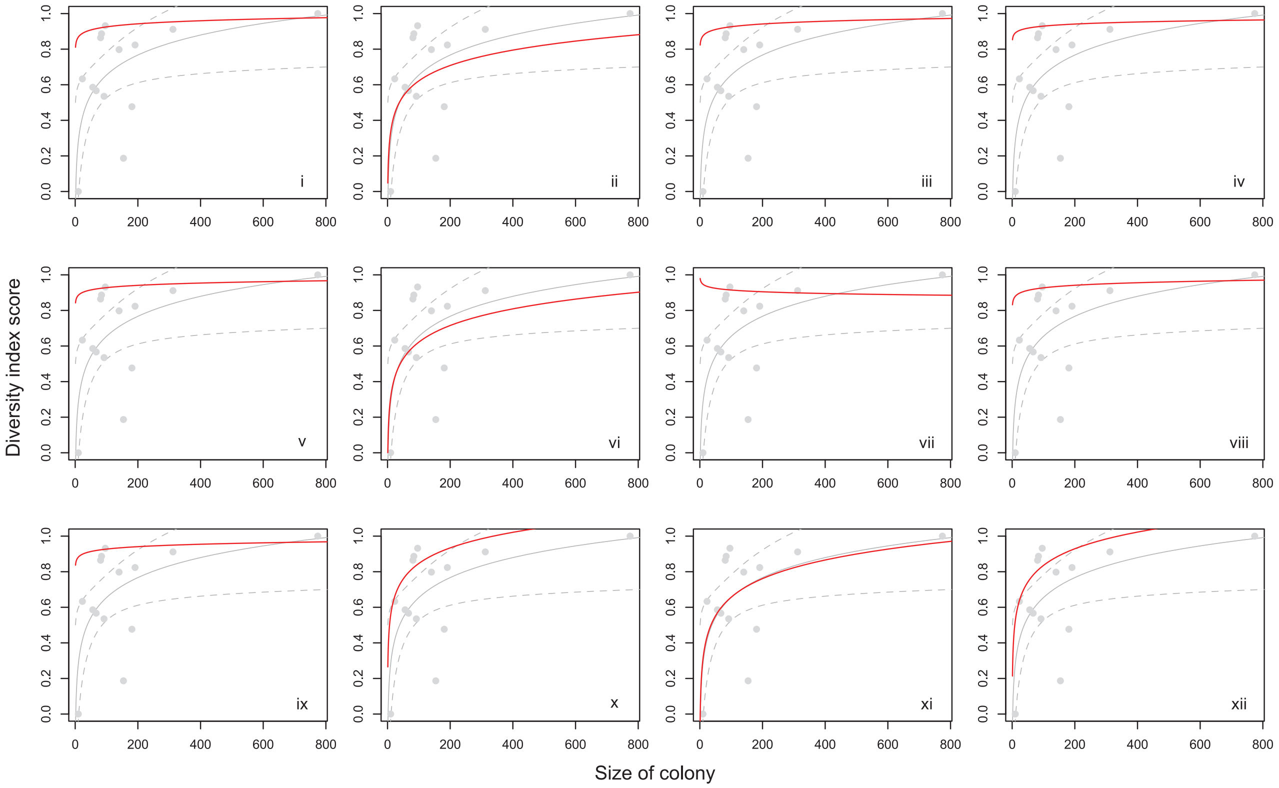

Figure 6

Comparison of the fit for each rule to the observed data. Each panel represents the relationship between colony size and diversity for one rule (numbered i–xii, see Table 2). The best supported rules were rule (ii), rule (vi), and rule (xi), which all incorporate conspecific attraction, with conspecific repulsion added to the second, and both conspecific and heterospecific repulsion added to the third rule. Relationship in simulated data for each rule is given by the red line. Gray points and lines in each panel are the observed data from Figure 3a.

predators (Davies et al. 2012). Our best-fitting rule also suggests that colonies have a maximum size (in this case 158 conspecifics or 289 conspecifics and heterospecifics overall), beyond which the costs exceed the benefits. This is consistent with our findings: 1) there was no significant relationship between nesting potential and colony size, which suggests these were potentially limited through avoidance and 2) we found an upper colony size limit beyond which there was no active attraction, suggesting that dilution of predation risk plays little role in driving these aggregations.

Our study suggests that an individual weaver may have 2 potential dimensions to consider: 1) nest with enough conspecifics to attract females to your colony, but 2) not too many so as to dilute your chances of reproductive success. These 2 rules alone, irrespective of the distribution of heterospecifics, appears to be enough to recreate realistic patterns of colony structure. Although this decision-making process may be challenging to test in weavers, other colonial species may use a similar decision-making process. For example, male zebra finches (*Poephila guttata*) responded to social stimulus (playback) simulating a larger colony by singing more (Waas et al. 2005). Varying female availability, and thus competition for resources, should cause a shift in the parameters of the model, suggesting a change in optimal colony size.

One aspect that was not considered in our models is whether asymmetries amongst individuals could lead to the observed variance in colony size (Brown et al. 1990). For example, high quality individuals (those displaying strong sexual signals) may have a higher competition threshold resulting from their higher competitive ability, leading to differences in their optimal colony size and subsequent joining rules. At first glance, our results suggest that simple joining rules by identical individuals are enough to recreate the observed patterns of colony size in conspecifics, without the need for individual variation. Our approach could also be used to investigate predictions of individual quality and spatial positioning within colonies that are related to hypothesized variation in information quality or predation risk (Brown et al. 1990) or linked to phenotypic assortment (Spottiswoode 2007). For example, do dominants reduce risk by prioritizing larger colonies or those in which they can be central? Finally, brood parasitism may also play a role in decision making. Nests that are central in a colony may be safer from brood parasites, such as Diederik cuckoos (*Chrysococcyx caprius*), but may be more prone to conspecific egg dumping by nearby nesting females (Jackson 1993). If the cost and benefit trade-off that arises from different types of parasitism varies between males and females, this could lead to the intriguing possibility that female choice could influence male decision making in terms of nest-site and colony suitability.

In this study, we have provided evidence that the distribution of species within and between mixed breeding colonies can arise primarily from conspecific attraction. A simple rule that is based on choosing an optimal colony with respect to conspecifics only was best supported. However, although we found no evidence for heterospecific attraction, our simulation approach does not suggest that mixed-species colonies did not evolve from mutual benefits, such as dilution of predation risk, between species. This is because we did not vary the overall distribution of nests between trees or incorporate other possible trees in which no colony was found. However, we do provide evidence that once this process has evolved (for example colony trees are established), the pattern of species diversity can be replicated with striking simplicity.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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Cooperation facilitates the colonization of harsh environments

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Animals living in harsh environments, where temperatures are hot and rainfall is unpredictable, are more likely to breed in cooperative groups. As a result, harsh environmental conditions have been accepted as a key factor explaining the evolution of cooperation. However, this is based on evidence that has not investigated the order of evolutionary events, so the inferred causality could be incorrect. We resolved this problem using phylogenetic analyses of 4,707 bird species and found that causation was in the opposite direction to that previously assumed. Rather than harsh environments favouring cooperation, cooperative breeding has facilitated the colonization of harsh environments. Cooperative breeding was, in fact, more likely to evolve from ancestors occupying relatively cool environmental niches with predictable rainfall, which had low levels of polyandry and hence high within-group relatedness. We also found that polyandry increased after cooperative breeders invaded harsh environments, suggesting that when helpers have limited options to breed independently, polyandry no longer destabilizes cooperation. This provides an explanation for the puzzling cases of polyandrous cooperative breeding birds. More generally, this illustrates how cooperation can play a key role in invading ecological niches, a pattern observed across all levels of biological organization from cells to animal societies.

Species breeding in cooperative groups are more commonly found living in hot and unpredictable environments (Fig. 1)[1–4]. This well-documented relationship has long been taken as evidence for the intuitively satisfying idea that harsh environments favour the evolution of helping behaviour[2–6]. The theoretical argument is that in harsh environments individuals are better off helping others with whom they share genes, either because independent breeding is likely to fail[5,7,8], or because helpers provide greater benefits when environmental conditions are worse[9,10]. This idea, often referred to as the 'ecological constraints hypothesis'[5,11], has been supported by a number of within-species studies showing individuals are more likely to breed cooperatively when environmental factors limit independent breeding[3,4,12–14], and that helpers provide insurance against breeding failure during poor years, which are frequent in harsh environments[9,10].

The idea that environmental conditions drive the evolution of cooperative breeding could, however, be incorrect. An alternative explanation is that causation is in the opposite direction, with cooperative breeding allowing individuals to colonize and breed in harsher environments. Another potential explanation is that there is no causal relationship between environmental conditions and cooperative breeding, and that their association is instead explained by a third correlated variable[15]. For example, environmental conditions can influence rates of divorce and female polyandry, both of which determine within group relatedness[16,17]. Relatedness is important because cooperation is more likely to be favoured if it is directed towards relatives that share the genes for cooperation[18], termed kin selection[19]. In this case, cooperative breeding could occur more often in harsh environments simply because the environment determines rates of female polyandry and relatedness within families, rather than environmental conditions directly selecting for helping behaviour. These competing hypotheses have remained untested because reliably reconstructing the order of evolutionary events for more than two traits simultaneously is a major challenge and requires data on the all relevant variables for a large number of species[20].

Here we conducted an analysis across birds that allowed us to test the different competing explanations driving the relationship between cooperative breeding behaviour and environmental harshness. We collected data on the breeding system of 4,707 species, defining them as either cooperative ($n_{\text{species}} = 154$) or noncooperative ($n_{\text{species}} = 4{,}553$) breeders depending on the presence of one or more non-breeding helpers at 10% or more of nests. This excludes communal breeders (for example, purple swamphen, *Porphyrio porphyrio*, and greater ani, *Crotophaga major*) and cooperative polygamists (such as the Galapagos hawk, *Buteo galapagoensis,* and brown skua, *Catharacta lonnbergi*), where all adults in the group typically reproduce, since we are concerned with explaining cooperation where individuals forego their own reproduction. This dataset allowed us to identify the points at which transitions to and from cooperative breeding have occurred in birds. We combined these data with information on both the environmental conditions species experience (mean, variance and predictability[21] in temperature and rainfall) and levels of female polyandry ($n_{\text{cooperative species}} = 45$, $n_{\text{noncooperative species}} = 263$). The environmental variables were highly correlated and so we used phylogenetic principal component analyses to create indices of environmental variation (Supplementary Table 1). The first principal component (environmental PC1) was strongly related to high mean temperature (factor loading = 0.76), low between-year variation in temperature (factor loading = −0.75), and high between-year variation in rainfall (factor loading = 0.69). For consistency with previous research, we refer to environmental

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Figure 1 | Animals living in harsh environments are more likely to breed cooperatively. a–d, For example, honeypot ants, *Myrmecocystus* spp.[1] (**a**) (photo © John Brown/Oxford Scientific/Getty Images), meerkats, *Suricata suricatta* (**b**) (photo by A.S.G.), snapping shrimp, *Synalpheus regalis*[30] (**c**) (photo courtesy of J. E. Duffy) and superb starlings, *Lamprotomis superbus*[4] (**d**) (photo courtesy of D. R. Rubenstein) are all able to inhabit environments where independent breeding is difficult. However, it remains unknown whether the environment selects for cooperative breeding or cooperative breeding facilitates the colonization of such harsh environments.

PC1 as environmental harshness, where high values indicate hot environments with variable rainfall (referred to simply as 'harsh') and low values represent cooler environments with lower variation in rainfall (referred to as 'benign')[16,22]. To tease apart the causality of the relationships between environmental conditions, cooperative breeding and polyandry, we estimated phylogenetic correlations, ancestral states and transition rates between variables using a combination of three phylogenetic techniques: multi-response Bayesian phylogenetic mixed models (BPMMs), reverse-jump Markov chain Monte Carlo transition rate models (rjMCMC), and phylogenetic path analysis.

Results

Our analyses confirm that cooperative breeding in birds is positively correlated with environmental harshness (Fig. 2 and Supplementary Table 2: BPMM phylogenetic correlation (phylo r) = 0.40, credible interval (CI) = 0.18 to 0.68, P_{MCMC} (number of iterations when one level is greater or less than the other level divided by the total number of iterations) = 0.001) and negatively correlated with rates of polyandry (Supplementary Table 2: phylo $r = -0.34$, CI = −0.53 to −0.03, $P_{\mathrm{MCMC}} = 0.01$). However, there was no apparent correlation between environmental conditions and rates of polyandry (Supplementary Table 2: phylo $r = 0.14$, CI = −0.21 to 0.44, $P_{\mathrm{MCMC}} = 0.22$). We also found the same patterns using analyses that estimated the evolutionary transition rates between cooperative and noncooperative breeding, environmental conditions, and rates of polyandry, which indicated that cooperative breeding has coevolved with environmental conditions and rates of polyandry, but that polyandry and environmental conditions have evolved independently (rjMCMC models of correlated versus independent evolution: cooperative breeding and environment, Bayes Factor (BF) = 11.12; cooperative breeding and polyandry, BF = 2.96; environment and polyandry, BF = 0.84—where BF > 2 offers positive evidence, >5 provides strong evidence, and >10 is very strong evidence). These analyses demonstrate that the association between cooperative breeding and environmental harshness is not simply a spurious relationship driven by female polyandry.

Next we examined the likely causality of the relationship between cooperative breeding and environmental traits by reconstructing the most likely environmental niches prior to cooperation evolving, and by examining transition rates to cooperative breeding from species with different environmental niches. We found no support for the hypothesis that living in harsh environments selects for cooperative breeding. The ancestral state reconstructions indicated that the ancestors of cooperative species occupied similar environmental niches to ancestors of noncooperative species (Fig. 3 and Supplementary Table 3; BPMM: environment of ancestors of noncooperative species = 0.62, CI = −0.48 to 1.57; environment of ancestors of cooperative species = 0.58, CI = −0.85 to 1.89; difference $P_{\mathrm{MCMC}} = 0.50$). Examining transition rates, we found that the transition from noncooperative to cooperative breeding was higher in species occupying benign rather than harsh environmental niches, where benign and harsh were classified as either the <70% or >70% quartile of environmental PC1, respectively (see the Methods for an explanation and assessment of sensitivity to thresholds; Supplementary Table 4; rjMCMC: benign conditions mean ± SD = 0.02 ± 0.005; percentage of models where transition did not occur, which gives an indication of how likely the transition is to take place (Z) = 1.1%; harsh environments = 0.01 ± 0.02, Z = 44.7%). Importantly, our analyses were not hindered by an inability to reconstruct the environmental niches ancestors occupied, as there was a strong phylogenetic signature in environmental

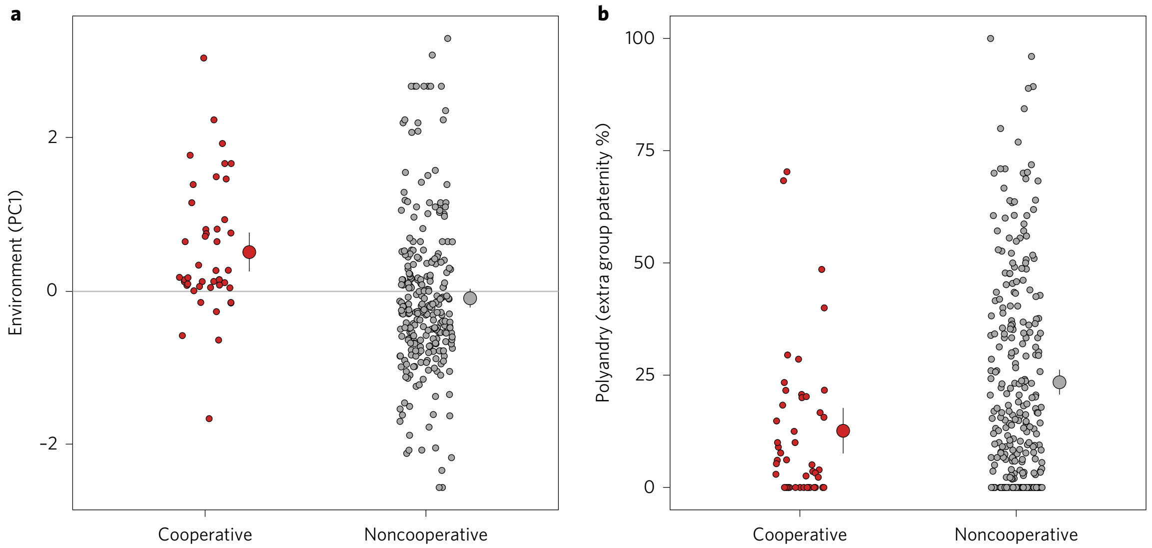

Figure 2 | Cooperative breeding and the association with harsh environments and low levels of polyandry. a, Cooperative breeders occur in environments that are hotter with more variable rainfall. Higher values of PC1 indicate higher mean temperatures, factor loading = 0.76, and greater between-year variance in rainfall, factor loading = 0.69: BPMM $n_{\text{cooperative}} = 45$, $n_{\text{noncooperative}} = 263$, $P_{\text{MCMC}} = 0.001$. 28% of species are cooperative in harsh environments (environmental PC1 > 70% quantile), whereas only 7% are in benign environments (environmental PC1 ≤ 70% quantile), equating to a fourfold difference. **b**, In noncooperative species, three times the number of nests have polyandrous females relative to cooperative species ($P_{\text{MCMC}} = 0.01$). Small dots represent species averages, and large dots with error bars represent mean ± 95% confidence intervals.

PC1, both when estimating this across all species (Supplementary Table 2; BPMM: phylogenetic heritability = 71%, CI = 51% to 84%) and when estimating this separately for cooperative and noncooperative species (Supplementary Table 5; BPMM: phylogenetic heritability for cooperative species = 68%, CI = 27 to 91%; phylogenetic heritability for noncooperative species = 84%, CI = 65 to 90%).

Although there was no support for harsh environmental conditions explaining the evolution of cooperative behaviour, we found strong support for the hypothesis that cooperative breeding facilitates the transition to living in harsh environments. The transition rate from living in benign environments to living in harsh environments was twice as high in cooperative as opposed to noncooperative breeders (Fig. 3 and Supplementary Table 4; rjMCMC: cooperative breeders = 0.05 ± 0.03, Z = 2.7%; noncooperative species = 0.02 ± 0.01, Z = 1%). Furthermore, when we conducted a phylogenetic path analysis that tested alternative models of the relationships among cooperative breeding, environmental conditions and polyandry, we found that the best-supported model was one where transitions to cooperative breeding preceded transitions to living in harsh environments (Supplementary Fig. 1 and Supplementary Table 6; best supported model Fisher's *C* statistic = 0.25, degrees of freedom (d.f.) = 2, *P* = 0.88). Taken together, our results strongly suggest that cooperative breeding facilitates living in harsh environments, and not that living in harsh environments favours cooperation (Fig. 3). What, then, explains the transition to cooperative breeding in birds?

Previous research on social insects[23], mammals[24] and birds[25] has suggested that monogamy or low levels of polyandry has played a key role in the evolution of complex social behaviour. Low levels of polyandry leads to high relatedness within family groups, which increases the kin-selected benefits of helping raise family members[26]. In support of this hypothesis and consistent with previous research, we found that the ancestors of cooperative species had significantly lower levels of polyandry than those of noncooperative species (Fig. 3 and Supplementary Table 3; BPMM: noncooperative species = 0.20, CI = 0.07 to 0.55; cooperative species = 0.04, CI = 0.004 to 0.38; difference $P_{\text{MCMC}} = 0.03$). Similarly to environmental PC1, ancestral levels of rates of polyandry could be estimated due to the high phylogenetic signature in this trait (Supplementary Table 2; phylogenetic heritability = 77.12%, CI = 59.52 to 87.70%).

There are, however, a number of relatively polyandrous cooperative breeders (Fig. 2). For example, 70% of nests of Australian magpies, *Gymnorhina tibicen* (Supplementary Table 13), and 40% of nests of western bluebirds, *Sialia Mexicana* (Supplementary Table 13), contain chicks fathered by males outside the social group. There are at least two, non-mutually exclusive, explanations for why cooperative breeding persists in such polyandrous species. One possibility is that cooperative breeding may evolve from polyandrous species if they live in harsh environments. That is, if harsh environments restrict the opportunities for independent breeding, then individuals may be selected to stay and help, even if the breeding female is polyandrous. Another possibility is that cooperative breeders can become more polyandrous if they live in harsh environments where it is difficult for helpers to desert and breed on their own. Although both explanations are based on similar reasoning, there is one key difference: the former hypothesis involves harsh environments facilitating the transition to cooperative breeding when species are polyandrous, whereas the latter hypothesis involves harsh environments 'trapping' species as cooperative breeders.

We did not find consistent support for the hypothesis that harsh environments facilitate the evolution of cooperative breeding in polyandrous species. Our transition rate analysis indicated that evolution of cooperative breeding increased from 0.00 ± 0.00 (Z = 100%) in benign environments to 0.02 ± 0.01 (Z = 4%) in harsh environments (Supplementary Table 4), suggesting that cooperative breeding can potentially evolve from polyandrous species when environmental conditions are harsh. However, if this hypothesis is true, then rates of polyandry should be positively associated with harsher environmental conditions in the ancestors of cooperative breeders. We tested this prediction by extending our BPMM models to estimate the correlation between environmental niches and rates of polyandry separately for each of the different transitions to cooperative breeding, and found no support for this prediction (Supplementary Table 7; BPMM: phylo *r* = −0.23, CI = −0.66 to 0.79, $P_{\text{MCMC}} = 0.49$). Taken

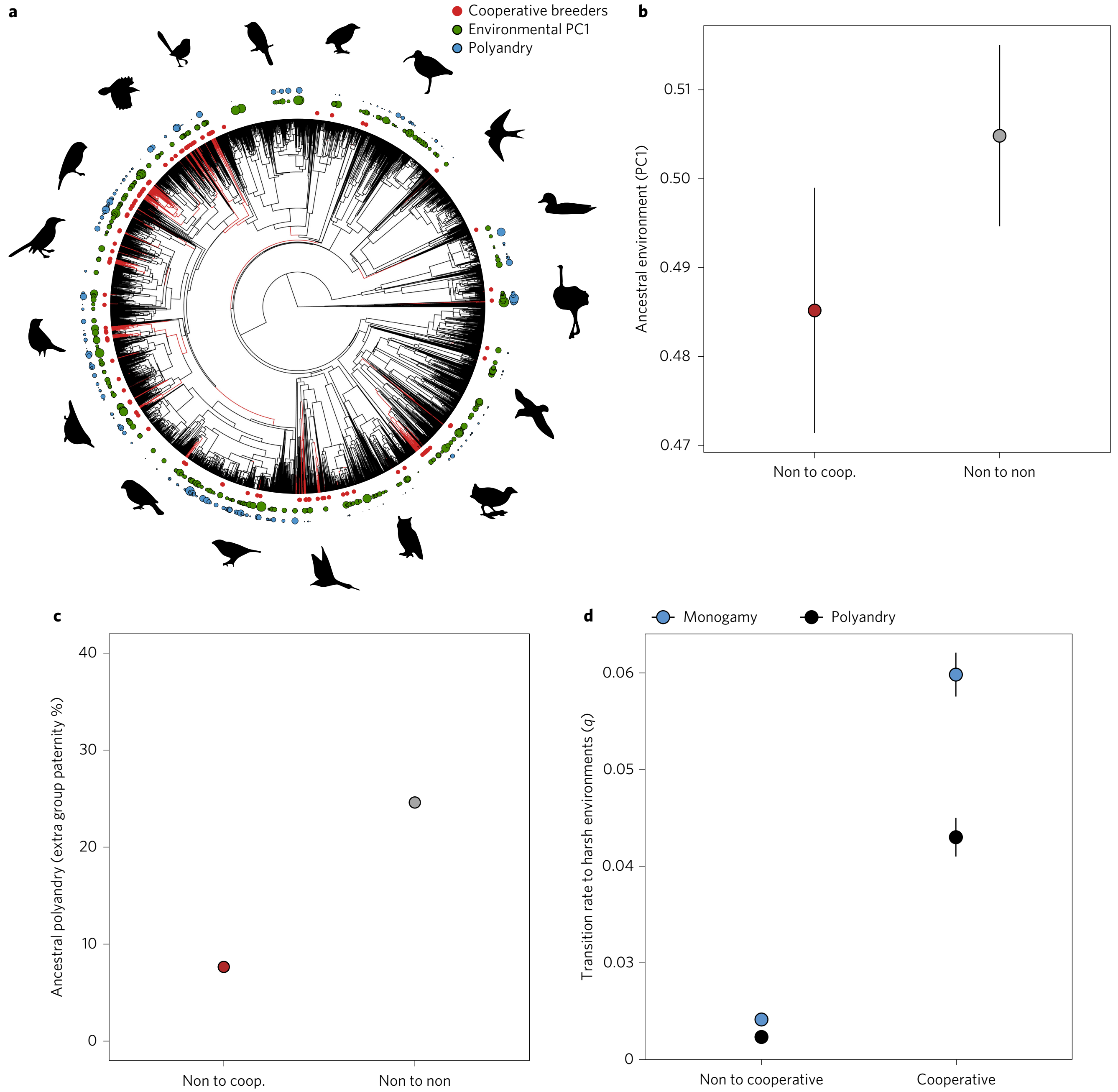

Figure 3 | Cooperation and the invasion of harsh environments. **a**, The phylogenetic distribution of the transitions to cooperative breeding (red circles; $n_{\text{species}} = 154$) and their relationship to environmental conditions (green circles; larger size = harsher environment) and polyandry (blue circles; larger size = higher levels of polyandry). Red branches are estimated transitions to cooperative breeding. **b**, Estimated environmental niches occupied by noncooperative (Non) ancestors to cooperative (Coop.) and noncooperative descendents. The number of transitions from noncooperative to cooperative breeders (range across 10 MCC trees): 52 to 122. Number of transitions from noncooperative to noncooperative breeders (range across 10 MCC) trees: 7,476 to 8,794. Difference between environments, $P_{\text{MCMC}} = 0.49$. Dots represent mean ± 95% confidence intervals. **c**, Estimated levels of polyandry of the noncooperative ancestors to cooperative and noncooperative descendents (difference in levels of polyandry $P_{\text{MCMC}} = 0.03$). **d**, The evolutionary transition rates from benign to harsh environmental niches from monogamous (blue) and polyandrous (black) cooperative and noncoooperative species estimated using BayesTraits rjMCMC. Plots in **b** and **c** were drawn using the posterior samples of the BPMMs, and **d** from the posterior samples from the BayesTraits rjMCMC analysis. Dots represent mean ± 95% confidence intervals.

together, these results suggest that, although possible, polyandrous species living in harsh environments do not tend to evolve into cooperative breeders.

In contrast, there was clear support for the prediction that rates of polyandry increase after species have become 'trapped' as cooperative breeders by harsh environments. We found that transitions from monogamy to polyandry in cooperative breeders were twice as high in harsh relative to benign environments (Fig. 4 and Supplementary Table 4; rjMCMC: harsh environments = 0.05 ± 0.03, Z = 2.5%; benign environments = 0.03 ± 0.03, Z = 2%). This result was not simply due to the effect of the environment on polyandrous behaviour, as there was no difference across noncooperative species (Fig. 4 and Supplementary Table 4; rjMCMC: harsh environments = 0.05 ± 0.04, Z = 2.6%; benign environments = 0.05 ± 0.03, Z = 0%).

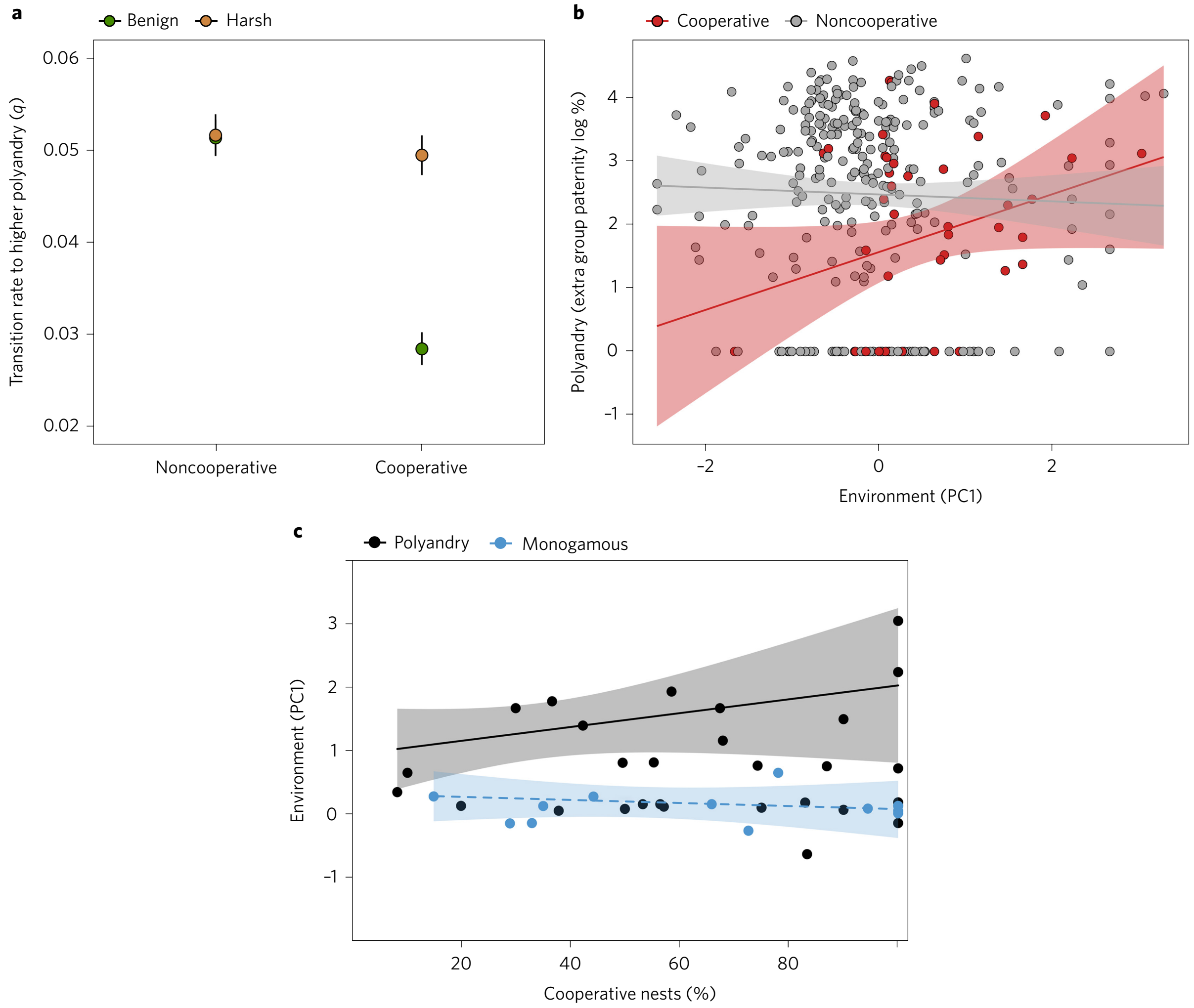

Figure 4 | The release of constraints on female polyandry in harsh environments. a, The transition rate from monogamy to polyandry was higher in cooperative species living in harsh environments (brown) than benign environments (green), but did not differ across noncooperative species. Plots were drawn using the posterior samples from the BayesTraits rjMCMC analysis. Dots represent mean ± 95% confidence intervals. **b**, Cooperative breeders living in harsh environments tend to be more polyandrous than cooperative species occupying more benign environments (red; $n_{\mathrm{species}} = 45$). In contrast, there was no relationship between environmental conditions and polyandry across noncooperative breeders (grey; $n_{\mathrm{species}} = 263$). Cooperation × polyandry $P_{\mathrm{MCMC}} = 0.05$. Dots represent species averages and fitted lines are mean regression slopes with 95% confidence intervals. **c**, Species with a higher percentage of nests with a least one helper inhabited harsher environments and were more polyandrous (black) than species living in benign environments that were more monogamous (blue; $n_{\mathrm{species}} = 43$ split into polyandrous and monogamous for graphical purposes only). Dots represent species averages. Fitted lines are from 90th percentile quantile regressions with 95% confidence intervals.

The result that harsh environments allow female cooperative breeders to evolve higher rates of polyandry was supported by a series of complementary analyses. We found that polyandrous cooperative breeders inhabit harsher environments than monogamous cooperative breeders, whereas the rates of polyandry in noncooperative species were similar across environments (Fig. 4 and Supplementary Table 8; BPMM, cooperation × polyandry = −0.31, CI = −0.61 to 0.05, $P_{\mathrm{MCMC}} = 0.05$). We then examined variation in the frequency of helping across cooperative species, as measured by the proportion of nests with helpers. We found that species that can cope with harsher environmental conditions had a significantly higher proportion of nests with helpers and higher rates of polyandry (Fig. 4 and Supplementary Table 8: BPMM, cooperation × polyandry = −2.37, CI = −3.40 to −1.14, $P_{\mathrm{MCMC}} = 0.0002$). Using quantile regression, which examines the effect of explanatory variables at different quantiles of the response variable, we found similar results: rates of helping behaviour and polyandry were most strongly and positively related to the upper quantiles of environmental PC1 (Fig. 4c, Supplementary Fig. 2 and Supplementary Tables 9 and 10: quantile regression, 50th percentile regression coefficient ± SE = 0.13 ± 0.17, $P = 0.44$, 95th percentile regression coefficient ± SE = 0.98 ± 0.40, $P = 0.02$; see Methods for details). This suggests that species with a higher frequency of helping can occupy the full range of environments, whereas when helping is rare, species are generally only found in benign environments (Fig. 4c). Additionally, it supports the idea that inhabiting harsh environments is associated with higher rates of polyandry (Fig. 4c). Overall, these results indicate that polyandrous cooperative breeders evolve from relatively monogamous cooperative breeders that live in harsh environments. This pattern echoes that observed with eusocial insects where polyandry evolved following the development of sterile workers, most likely because sterile workers are unable to desert and reproduce themselves[23,26].

Within our dataset of 4,707 species, cooperative breeding has also been lost approximately 82 times (range across 10 different maximum clade credibility trees = 54 to 116). One potential explanation

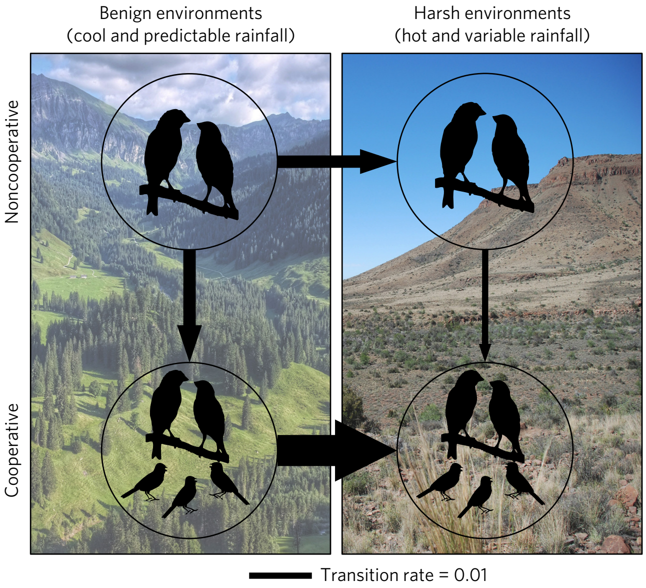

Figure 5 | Evolutionary transitions between cooperative breeding and environmental niches. Cooperative breeding is more likely to evolve in species occupying benign environment niches, which subsequently facilitates the invasion of hot environments with variable rainfall. Width of arrows indicate transition rates estimated using rjMCMC implemented in BayesTraits. Image credits: left, photo courtesy of Stijn Te Strake; right, photo by C.K.C.

for these losses of cooperation is that female polyandry has increased in species that live in benign environments, causing helpers to desert and breed alone. However, there was no clear evidence to explain why cooperation breaks down, either by jointly modelling the effects of polyandry and the environment using ancestral state reconstruction analyses (Supplementary Table 11) or by estimating the transition rates from cooperative to independent breeding in harsh versus benign environments from monogamous and polyandrous ancestors (Supplementary Table 4). One potential issue is that there is only data on female polyandry for species involved in just 5 out of the 82 losses. As a result, the breakdown of cooperative breeding across birds remains enigmatic for the moment—but, from our analyses, it is clear that in order to resolve this mystery we need more data on cooperative species that are basal to noncooperative breeders, especially information on rates of polyandry and environmental niches (Supplementary Table 12).

Discussion

Overall, our results overturn the accepted explanation for why cooperative breeding species tend to be found in harsher environments, namely that the benefits of helping are greater when environmental conditions are worse. Instead, our analyses suggest that cooperative breeding evolves from monogamous species in relatively benign environments (Fig. 2 and Fig. 5), which then enables species to colonize harsh environments (Fig. 3 and Fig. 5). More generally, our results illustrate how cooperation can influence evolution at a macro scale, by allowing species to colonize new environments. The idea that cooperation can aid pioneering into environments uninhabitable for individuals may occur at all levels of life. The formation of cooperative associations, such as biofilms, enable bacteria to survive in harsh environments and resist antibiotic attack[27]. The cooperative formation of multicellular organisms, with division of labour between cell types, has allowed exploitation of environments in numerous ways[28,29]. The evolution of sociality in insects and sponge-dwelling shrimps has allowed these diverse organisms to become keystone species in diverse habitats from jungles to oceans[1,30,31]. The acquisition of bacterial symbionts has facilitated the colonization of novel niches, from sap-feeding aphids to worms in deep-sea hydrothermal hot vents[32]. Together these results show how cooperation has played a key role in adaptive breakthroughs that have opened up new ecological niches.

Methods

Data collection on breeding system. All species used in the analyses are listed in Supplementary Table 13, which uses Latin names listed in the International Ornithological Congress (IOC) master list v2.3. We categorized species as cooperative or noncooperative across the phylogeny for which there was available data (Supplementary Table 13: $n_{\text{species}} = 4{,}707$, of which 154 were cooperative). We collected data by starting with major review articles that have classified the breeding systems of birds[33,34], and then subsequently checked the primary literature to determine whether species classed as cooperative met our criteria. We classed species as cooperative when at least 10% of the nests in a population had at least one sexually mature, non-breeding helper, as we are concerned with explaining why individuals give up reproductive success to help others. In the vast majority of species, these constituted retained natal offspring. We excluded species where sample sizes were not given or information was anecdotal.

Categorizing species as cooperative or noncooperative captures large differences and is analytically tractable, but inevitably misses the finer details of species characteristics. Therefore, to gain more precise information on the cooperative behaviour of species, we searched for published data on the number of nests that were provisioned by pairs versus the number of nests assisted by helpers in populations ($n_{\text{species}} = 43$). Wherever possible, we used estimates from the same study populations as those where extra-group paternity was measured (Supplementary Table 14).

Data collection on polyandry. We collected data on female mating behaviour from published studies (see ref. [25] for more details). Two highly correlated statistics (Pearson's Correlation coefficient = 0.90, confidence interval = 0.88 to 0.92, $n = 304$, t-test = 36.55, $P < 0.0001$) are frequently reported in parentage studies with respect to multiple paternity: (i) the percentage of chicks fathered by extra-pair/extra-group fathers; and (ii) the percentage of broods with one or more extra-pair/group chicks. We analysed data on the percentage of broods in the population containing extra-group offspring, which we refer to as 'polyandry' (in previous publications we have referred to this as promiscuity[25,35]). We chose the percentage of broods rather than the percentage of chicks with extra-group paternity as it is less susceptible to extreme values from individual nests, thereby providing a more robust estimate of population levels of female multiple mating. Moreover, we focused on extra-group paternity as we are concerned with behaviour that reduces relatedness between offspring and all individuals caring for offspring. Rates of within-group extra-pair paternity are extremely low in cooperative breeders when defined as 'species with one or more non-breeding adults helping to raise offspring', as helpers are typically retained natals[35]. In species without a pair bond (for example, lekking and parasitic species), we have used data on the proportion of nests containing offspring fathered by more than one male.

We compiled data on polyandry by updating the dataset published in ref. [25] to include recently published data (up to and including 15 October 2015). We searched for new studies on extra-group paternity data in birds by entering the following search terms into the Web of Science keywords search: (1) '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'; (2) title 'parentage' AND topic 'birds'; (3) title 'mating system' AND 'birds'; and (4) all references that cite the two major reviews on extra-pair paternity in birds[36,37]. For several species there were multiple studies that measured polyandry, and for these we calculated the mean value of the studies weighted by sample size for use in subsequent analyses (Supplementary Table 14). In some cases there were multiple studies presenting paternity data from the same study population over the same years. To avoid duplication, we only used information from the paper with the largest sample size.

Data collection on the environment. For each study on paternity, we extracted the geographical coordinates and used these to extract climatic data for the population. Precipitation and temperature data were obtained from the University of East Anglia Climatic Research Unit's Time series dataset, CRU-TS 3.21[38]. The mean and variances for each environmental parameter were computed annually and then averaged across years at each site. Predictability was measured via Colwell's P (ref. [21]), an index that captures among-year variation in onset, intensity and duration of periodic phenomena ranging from 0 (completely unpredictable) to 1 (fully predictable). When multiple studies were available for a given species, environmental variables were first characterized locally and then averaged across sites for the species. Where paternity was measured in multiple populations, we extracted climate data for each population and used this to calculate an average for the species.

Phylogenetic trees. We used the complete phylogeny of birds ($N_{\text{species}} = 9{,}993$, 10,000 posterior tree samples) available at www.birdtree.org with the Hackett backbone[39] and pruned it to the 4,707 species for which we had breeding data. Out of the 308 species for which we had complete data, all but 8 were present in the genetically sequenced phylogeny available from ref. [39].

We accounted for phylogenetic uncertainty in our analyses in two ways. First, for our Bayesian phylogenetic mixed models (BPMMs; see below for details), we used the 10,000 posterior tree samples to create 10 maximum clade credibility (MCC) consensus trees, each constructed from 1,000 different posterior samples, using Tree Annotator v2.0.3[40]. We repeated each analysis 10 times, each time with a different tree, and combined the posterior samples generated from each tree prior to parameter estimation. We used this approach for the BPMMs because at the time of analysing our data we were unaware of any techniques for resampling across a set of trees within a single analysis. Second, for our transition rate analysis using BayesTraits, it was possible to take phylogenetic uncertainty into account by resampling each iteration from a posterior distribution of 1,000 trees for the 4,707 species in our dataset, therefore negating the need to create MCC trees.

Statistical analyses. Unless otherwise stated, all analyses were conducted in R v3.1.0[41]. All data figures were made in R.

Data set construction. Prior to the analyses we created an index of environmental conditions using a phylogenetic principle component analysis (PCA) from the mean, variance and Colwell's predictability estimates of temperature and precipitation. Separate phylogenetic PCAs were run for each of the 10 MCC trees and used to create 10 datasets that were then used in subsequent analyses. All explanatory variables were Z-transformed (mean centred with standard deviation = 1) prior to analyses. Where polyandry was used as an explanatory variable, it was arcsine square root transformed before the analysis, as it is percentage data.

General model settings, model assessments and parameter estimation. *Bayesian phylogenetic models.* We used the MCMCglmm package v2.20 to implement BPMMs with Markov chain Monte Carlo (MCMC) estimation[42]. We estimated the number of iterations, burn-ins and thinning intervals required for each analysis using the MCGIBBSIT package v1.1.0[43]. Each model was run for 6,000,000 iterations with a 1,000,000 burn-in and chains sampled every 1,000 iterations unless otherwise specified. We examined the convergence of models by repeating each analysis three times and examining the correspondence between chains using the 'coda' package version 0.16-1[44] in the following ways: (i) visually inspecting the traces of the MCMC posterior estimates and their overlap; (ii) calculating the autocorrelation and effective sample size of the posterior distribution of each chain; and (iii) using Gelman and Rubin's convergence diagnostic test that compares within- and between-chain variance using a potential scale reduction factor (PSR)[45]. Values substantially higher than 1.1 indicate chains with poor convergence properties. The PSR was less than 1.1 for all the parameter estimates presented. We modelled the probability of cooperative breeding as a binary trait with a logit link function, environmental PC1 and PC2 as Gaussian traits, and polyandry as a binomial trait with logit link function (number of nests with extra-group chicks, number of nests without extra-group chicks).

The prior settings used for each analysis are specified in the R code in the Supplementary Information. For random effects, we began prior selection by assessing model convergence using inverse-Wishart priors ($V = 1$, $\nu = 0.002$). If the mixing properties of the MCMC chain were poor, which was often the case for binary response traits, we examined two different parameter expanded priors (Fisher prior: $V = 1$, $\nu = 1$, $\alpha.\mu = 0$, $\alpha.V = 1{,}000$) and (χ^2 prior: $V = 1$, $\nu = 1{,}000$, $\alpha.\mu = 0$, $\alpha.V = 1$)[46]. For binary traits, the residual variance cannot be identified and therefore we set the residual variance to 1, otherwise an inverse-Wishart prior was specified for residual variances ($V = 1$, $\nu = 0.002$). For fixed effects, the default priors in MCMCglmm (independent normal priors with zero mean and large variance (10^{10})) were used, apart from in models with logit link functions (binary and binomial response variables). In these models we specified a fixed effect prior of $\mu = 0$, $V = \sigma^2_{\text{units}} + \pi^{2/3}$, which is approximately flat on the probability scale when using logit link functions, and improved the mixing properties of the fixed-effect chains. (μ, mean; σ, standard deviation; V, variance; ν, the degree of belief parameter; α.μ, prior mean; α.V, prior covariance matrix.)

Parameter estimates from models are reported as the posterior modes with 95% lower and upper credible intervals (CIs). P values reported testing differences between levels (for example, cooperative versus non-cooperative breeders) are the number of iterations when one level is greater or less than the other level divided by the total number of iterations. P values reported for correlations (such as environmental conditions and the probability of being a cooperative breeder) are the number of iterations where the correlation is greater or less than 0 divided by the total number of iterations.

Specific analyses. We conducted the following specific analyses to quantify the relationships, and estimate causality, between cooperative breeding, environmental conditions and female polyandry.

Testing if cooperative breeding, environmental conditions and polyandry are correlated over evolutionary time. *Estimating phylogenetic correlations using MCMCglmm.* We used multi-response Bayesian phylogenetic mixed models (MR-BPMM) to estimate the phylogenetic and residual correlations between the probability of cooperative breeding, environmental PC1, environmental PC2 and rates of polyandry (Supplementary Table 3). We removed the global intercept to allow trait specific intercepts to be estimated and fitted 4 × 4 unstructured phylogenetic and residual covariance matrices as random effects. Correlations between traits were calculated as covariance between traits $xy/\sqrt{}$ (variance in trait x × variance in trait y). Since cooperative breeding is a binary trait, the residual variance is not identifiable and so it was not possible to estimate the residual correlations between cooperative breeding and the other traits. We also estimated the amount of variation in each trait explained by shared ancestry between species calculated as phylogenetic heritability (phylo H^2 = (phylogenetic variance/residual + phylogenetic variance) × 100) for environmental PC1, environmental PC2 and polyandry, and the intraclass correlation coefficient (phylogenetic variance/(phylogenetic variance + 1) + $\pi^{2/3}$) for cooperative breeding—an analogous measure of the amount of variation explained by phylogenetic history appropriate for binary traits.

Testing models of dependent versus independent evolution using BayesTraits. We tested if models that allowed for coevolution between the probability of cooperative breeding, environmental conditions, and polyandry better explained our data than models that assumed independent evolution of each trait using the Multistate module with reverse jump MCMC estimation implemented in BayesTraits v2[47]. We transformed environmental PC1 and polyandry into binary classifications as it is not possible to estimate transition rates using continuous variables. We choose the 30th/70th quantile boundary to split continuous variables into binary traits as this captured large biological differences between species while maintaining sample size in each combination of categories (number of cooperative species, monogamy benign = 12, monogamy harsh = 9, polyandrous benign = 12, polyandrous harsh = 12. Number of noncooperative species monogamy benign = 48, monogamy harsh = 24, polyandrous benign = 143, polyandrous harsh = 48). We examined the sensitivity of our results to different thresholds (50th/50th quantile boundary and 40th/60th quantile boundaries). The results from different thresholds were qualitatively similar supporting the same conclusions (Supplementary Table 4) and so we only presented the results from the 30th/70th quantile boundary.

We used the Multistate module in BayesTraits rather than the Discrete module, which is normally used to examine coevolutionary relationships as it only allows two traits to be modelled. We therefore coded the different combinations of the three traits as different states; for example, non-cooperative breeders living in benign environmental conditions with low rates of polyandry were classified as being in state 'A'. This resulted in eight different states, which were used to construct a rate matrix that allowed transitions between the two states of each trait against the different backgrounds of the other traits leading to 24 different transition rates being estimated. All other possible transitions between states were restricted to 0 to prevent dual transitions (for example, where there is a state change in two or more traits). The models of independent evolution, on the other hand, estimated transitions between the two states of each trait across the different levels of the two other traits. We used Bayes Factors (2 × (log(likelihood of complex model) − log(likelihood of simple model))) to test the fit of an independent model of evolution against four alternative coevolutionary models: (i) all traits coevolve; (ii) cooperative breeding only coevolves with environmental conditions; (iii) cooperative breeding only coevolves with polyandry; and (iv) only polyandry and environmental conditions evolve (Supplementary Table 4). It is commonly concluded that Bayes factors over 2 offer positive evidence, those over 5 provides strong evidence, and those over 10 is very strong evidence[47].

We used hyper priors where values were drawn from a uniform distribution with a range 0 to 10 to seed the mean and variance of a exponential prior to reduce uncertainty over prior selection[47]. The prior settings were chosen according to the estimated range of transition rates obtained using analyses with maximum likelihood estimation. We also examined the sensitivity of our models to prior selection by running models with gamma priors seeded using hyper priors and recovered similar results. We only present the results from the models using exponential priors as the mixing properties of the MCMC from these models were better than the other priors. We ran each model three times for a total of 6,000,000 iterations, a burn-in of 1,000,000 iterations and sampled every 5,000 iterations. Assessment of model convergence was carried out as described in the section 'General model settings, model assessments and parameter estimation'.

Estimating phylogenetic heritability of environmental PC1 for cooperative and noncooperative species separately using MCMCglmm. To accurately reconstruct the environmental conditions that the ancestors of cooperative and noncooperative species occupied, it is important that the environmental niches of cooperative and noncooperative species are equally conserved over evolutionary time. We examined this by quantifying the variation in environmental PC1 explained by phylogenetic history (phylogenetic heritability) separately for cooperative and noncooperative species using a BPMM. We fitted cooperative breeding as a fixed effect and removed the global intercept to allow separate means to be estimated for cooperative and noncooperative species. We fitted interactions between cooperative breeding and phylogenetic and residual variances as random effects using heterogeneous 2 × 2 covariance matrices where phylogenetic and residual variances are estimated separately for cooperative and noncooperative breeders and covariances are set to 0 (see R code in Supplementary Information for more details).

Examining the environmental conditions and levels of polyandry that preceded the evolution of cooperative breeding. *Ancestral state reconstructions using MCMCglmm*. We examined how the environmental conditions and levels of polyandry differed between ancestors of cooperative and noncooperative breeders using a two step approach: first, we reconstructed ancestral breeding states to predict transitions between cooperative and noncooperative breeding, and second, we tested whether transitions in breeding systems differed in their estimated environmental conditions and levels of polyandry. We reconstructed ancestral breeding states using a BPMM of the probability of cooperative breeding as the response variable and a phylogenetic variance-covariance matrix fitted as a random effect. Each model was run for 11,000,000 iterations with a 1,000,000 burn-in and chains sampled every1000 iterations. For each node in the phylogeny, this model produces a posterior probability of being cooperative. We classified nodes as being cooperative if the posterior probability was >0.9 and non-cooperative if it was <0.1, otherwise nodes were considered unknown. This leads to nodes being classified in four ways: (i) noncooperative node whose descendants are all noncooperative; (ii) noncooperative node with at least one descendant that is cooperative; (iii) cooperative node whose descendants are all cooperative; and (iv) cooperative node with at least one descendent that is noncooperative.

We entered the nodal classifications as an explanatory variable (four-level fixed factor) in a multi-response BPMM with environmental PC1 and polyandry as the response traits and a phylogenetic covariance matrix linked to ancestral nodes as a random effect (Supplementary Table 3). We removed the global intercept and fitted interactions between 'trait' and node classification to estimate environmental conditions and polyandry preceding the origin (comparison of classifications i versus ii), maintenance (comparison of classifications i versus iii) and loss of cooperative breeding (comparison of classifications iii versus iv). To account for uncertainty in our node classifications, we repeated the analysis 100 times, each 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 and from across the 10 different MCC trees to calculate parameter estimates. Each model was run for 20,000 iterations with a burn-in of 10,000 iterations and thinning interval of 1,000 samples, which across the resamplings and 10 different phylogenetic trees resulted in 10,000 posterior samples (10 trees × 100 resamplings × 10 samples per resampling).

Ancestral state reconstructions using MCMCglmm with transition-specific covariances between traits. The BPMM presented in the section 'Ancestral state reconstructions using MCMCglmm' fits a single phylogenetic covariance between environmental PC1 and polyandry that models the relationship between the environment and polyandry across all types of transitions in breeding system. As a result, it does not allow the possibility that the covariance between environmental PC1 and polyandry is different for different transitions. Theoretically, it is possible that cooperation may evolve from polyandrous ancestors when environmental conditions are harsh and independent breeding is constrained, as individuals have no other options of passing on their genes but through helping. In contrast, in benign environments it is predicted that cooperation will only evolve from monogamous ancestors because if breeding females are polyandrous then the indirect fitness benefits will be low and potential helpers will desert to breed on their own. If true, then we would expect the phylogenetic correlation between environmental conditions and polyandry to be significantly higher across the ancestors of cooperative species (nodal classification ii) than ancestors that only gave rise to noncooperative descendents (nodal classification i). We tested this idea by extending the BPMM outlined in the section 'Ancestral state reconstructions using MCMCglmm' to include transition specific phylogenetic variances and covariances between traits using the *at.level* coding in *MCMCglmm* (see the R code in the Supplementary Information for details). From these models we calculated whether the difference in the phylogenetic covariance between environmental PC1 and polyandry between transitions where cooperation evolved and transitions where noncooperative breeding was maintained (noncooperative ancestors to noncooperative descendents) was significantly greater than 0 (phylo $COV_{env\ PC1,\ polyandry}$ at.level(Non-Coop) - phylo $COV_{env\ PC1,\ polyandry}$ at.level(Non-Non): Supplementary Table 7). These models are extremely computer intensive. As a result we ran them for 25,000 iterations per tree with a burn-in of 5,000 iterations and thinning interval of 200 creating 1,000 posterior samples across the 10 different phylogenetic trees, which still resulted in all convergence criteria being met (see the section 'General model settings, model assessments and parameter estimation').

Calculating evolutionary transition rates using BayesTraits. We used the model in the section 'Testing models of dependent versus independent evolution using BayesTraits' that allowed coevolutionary relationships between all three traits to estimate the transition rates between states of cooperative breeding, environmental conditions and polyandry. We examined whether transitions to cooperative breeding differed according to benign and harsh environmental conditions, as well as in relation to monogamy versus polyandry. We examined the likelihood of transitions occurring by examining the proportion of models visited by the reverse jump MCMC algorithm where the rates were assigned to zero (Supplementary Table 7).

Testing alternative evolutionary causal models using phylogenetic path analysis. We used phylogenetic path analysis to examine alternative models of the causal relationships between cooperative breeding, environmental PC1 and polyandry (Supplementary Fig. 1). The alternative models we compared were constructed based on the correlations revealed by analysis in the section 'Estimating phylogenetic correlations using MCMCglmm' and distinguish between the following possibilities: (i) variation in polyandry predicts the probability of cooperative breeding which predicts the environments species occupy; (ii) variation in the environment explains the probability of cooperative breeding that in turn determines levels of polyandry; and (iii) cooperative breeding predicts the rates of polyandry and the environment species inhabit (Supplementary Fig. 1). For these analyses, we treated the probability of being a cooperative breeder as a Gaussian rather than a binary trait, as it has been shown this results in more accurate parameter estimation (see ref. [48] for justification for treating this variable as continuous). We also did not include environment PC2 in these models because there was no evidence from the analyses in section 'Estimating phylogenetic correlations using MCMCglmm' that it influenced any of the other variables.

We use the methods described in ref. [49] that integrate phylogenetic generalised least squares (PGLS) models, fitted using the R package 'Caper' v0.5.2[50], with the *d-sep* test outlined in ref. [51] to identify the model that best explained our data. In brief, a causal model is proposed that specifies how the variables are related in terms of dependent (changes in A cause changes in B) and independent (A and B are conditionally independent given variable C) effects. Each conditional independency is then tested using PGLS models to estimate the probability that the partial regression coefficient is 0 while taking into account the non-independence of data arising due to shared ancestry between species. The probabilities associated with each conditional independency can then be combined using Fisher's *C* statistic, which follows a χ^2 distribution with degrees of freedom equal to 2*the number of tests conducted. Furthermore, the fit of different models to the data, including non-nested models (as long as the dataset is the same for all models) can be compared using an Information Theory approach based on Fisher's C statistic (CICc):

$$\mathrm{CICc} = C + 2q \times n / (n - q - 1)$$

where C is Fisher's C statistic, n is the sample size and q is the number of parameters used to build models plus the number of relationships linking the parameters. If the proposed causal model fits the data then $P > 0.05$ for the C statistic and the model with the smallest CICc value represents the best candidate model out of the proposed set of models. For frequentist analyses such as these there is, to our knowledge, no established way of integrating results obtained across different trees to take into account phylogenetic uncertainty. We therefore repeated our analyses across the 10 MCC trees and averaged P values and regression coefficients across the 10 analyses (see ref. [20] for a discussion on averaging across phylogenetic trees).

Testing if cooperation and polyandry predict the environments species inhabit. *Calculating if the invasion of harsh environments is facilitated by cooperative breeding and polyandry using BayesTraits.* We used the model in the section 'Testing models of dependent versus independent evolution using BayesTraits' that allowed coevolutionary relationships between all three traits to estimate the transition rates between states of cooperative breeding, environmental conditions and polyandry. We examined whether transitions to harsh environments differed between cooperative and noncooperative breeders and in relation to monogamy versus polyandry. We again examined the likelihood of transitions occurring by examining the proportion of models visited by the reverse jump MCMC algorithm where the rates were assigned to zero (Supplementary Table 4).

*Testing if cooperative breeding and rates of polyandry predict the environments species inhabit using MCMCglmm.*We tested whether cooperative breeding and rates of polyandry were related to the environmental niches species can occupy using a BPMM with a Gaussian error distribution. We fitted environmental PC1 as the response variable, cooperative breeding (two-level factor: cooperative versus noncooperative), rates of polyandry (covariate) and clade (two-level factor: passerine versus nonpasserine) as fixed effects and a phylogenetic variance–covariance matrix as a random effect. We included all interactions among fixed effects to test whether the effect of cooperative breeding on the environments inhabited by cooperative and noncooperative species differed according to rates of polyandry and between passerines and nonpasserines. We included clade in this analysis because it has been suggested that the link between cooperative breeding and ecology is different for passerines and nonpasserines[2].

Testing if the degree of cooperation (percentage of nests with helpers) across cooperative breeders predicts the environments they inhabit and how polyandrous they are. *Tests using quantile regression.* Examining the relationship between levels of cooperation and environmental conditions is not straightforward as we expect that species with high levels of cooperation can occur in all environments, whereas less cooperative species will only inhabit more benign environments. We were therefore interested in testing whether levels of cooperation determine the upper environmental limit rather than the mean, which is typically estimated by regression analyses. As a result we used quantile regression implemented in the R package 'quantreg' v5.11[52], which splits the response variable, in this case environmental PC1, into different quantiles and estimates regression coefficients for each explanatory variable for each quantile. This procedure enables the change in regression coefficients and their confidence intervals to be estimated across the whole range of a response variable (Supplementary Fig. 2). If the upper limit of the environmental PC1 species occupy depends on levels of cooperation then we expect that the relationship between environmental niche and percent of cooperative nests will increase as data are restricted to higher quantiles of percent of cooperative nests (Supplementary Fig. 2 and Supplementary Table 10). We also included polyandry and its interaction with percent of cooperative nests in our quantile regression models to examine if polyandry increases when constraints on independent breeding are expected to be greatest (species occupy the most extreme environments and are obligately cooperative).

Tests using MCMCglmm. An important limitation of the currently available programs for performing quantile regression is that they do not allow modelling of phylogenetic relationships between species. We therefore verified our results from the quantile regression analysis by converting our continuous explanatory variables into categories (obligate (>90% nests have helpers) versus facultative (≤90% of nests with helpers) cooperative breeders, and monogamous (≤30% quantile of extra-group paternity) versus polyandrous (>30% quantile of extra-group paternity)) and performing a BPMM with environmental PC1 as the response variable, cooperative breeding and polyandry as two-level fixed factors and a phylogenetic variance-covariance matrix as a random effect. We once again tested if cooperative breeding allows species to occupy more extreme environments, and if this in turn relaxed constraints on female mating behaviour (because it makes independent breeding more difficult), by fitting an interaction between cooperation and polyandry.

Testing if increases in female polyandry in cooperative breeders are higher in harsh versus benign environments using BayesTraits. We extracted the estimated transition rates from monogamy to polyandry for cooperative breeders in benign versus harsh environments from the model in the section 'Testing models of dependent versus independent evolution using BayesTraits' that allowed coevolutionary relationships between all traits. We examined the likelihood of transitions occurring by examining the proportion of models visited by the reverse jump MCMC algorithm where the rates were assigned to zero (Supplementary Table 4).

Testing if the breakdown of cooperation is explained by increases in polyandry when environmental conditions are benign. *Estimating the environmental conditions and levels of polyandry in cooperative species with noncooperative descendants using MCMCglmm.* The analysis presented in the section 'Ancestral state reconstructions using MCMCglmm' allows environmental conditions and rates of polyandry to be compared between cooperative ancestors that only have cooperative descendants (maintenance of cooperation, nodal classification iii) and those that have noncooperative descendants (breakdown of cooperation, nodal classification iv). We found no evidence that the breakdown of cooperation was associated with differences in estimated environmental conditions or rates of polyandry (Supplementary Table 3). However, in the BPMM used in the section mentioned above, a single phylogenetic variance was fitted for each trait and only a single covariance for each trait combination (for example, environmental PC1:polyandry). This does not allow for the possibility that the covariance between traits is different between the maintenance of cooperation and the breakdown of cooperation. This is particularly important in this context because we predict that cooperation will breakdown when polyandry is high (low r) and environmental conditions are benign (low $b{:}c$). We predicted that this would be reflected in the phylogenetic covariance between polyandry and environmental PC1 being significantly more positive when cooperation is maintained (nodal classification iii) versus when cooperation is lost (nodal classification iv).

We used the models specified in the section 'Ancestral state reconstructions using MCMCglmm with transition specific covariances between traits' to calculate the differences in phylogenetic covariance between environmental PC1 and polyandry between transitions where cooperation was maintained and where cooperation was lost (phylo $COV_{env\ PC1,\ polyandry}$ at.level(Coop-Coop) − phylo $COV_{env\ PC1,\ polyandry}$ at.level(Coop-Non-coop)) (see Supplementary Table 11).

Estimating the rate of breakdown of cooperative breeding in relation to different environmental conditions and levels of polyandry using BayesTraits. We examined the rates of breakdown of cooperative breeding in relation to rates of polyandry and environmental conditions using the model described in the section 'Testing models of dependent versus independent evolution using BayesTraits' that allowed coevolutionary relationships between all traits. We examined the likelihood of transitions occurring by examining the proportion of models visited by the reverse jump MCMC algorithm where the rates were assigned to zero (Supplementary Table 4).

Code availability. The R code used to conduct analyses is supplied in the Supplementary Information.

Data availability. All data generated or analysed during this study are included within the paper and in the Supplementary Information.

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Author contributions

C.K.C., S.A., D.R.R. and A.S.G. conceived the study, C.K.C. analysed the data, C.A.B. and P.D. contributed materials, and all authors contributed substantially to writing the paper.

Additional information

Supplementary information is available for this paper.

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Competing interests

The authors declare no competing financial interests.