



# Big groups attract bad eggs: brood parasitism correlates with but does not cause cooperative breeding



Michael T. Wells<sup>a,\*</sup>, F. Keith Barker<sup>b,1</sup>

<sup>a</sup> Department of Ecology, Evolution and Behavior, University of Minnesota, St Paul, MN, U.S.A.

<sup>b</sup> Bell Museum of Natural History and Department of Ecology, Evolution, and Behavior, University of Minnesota, St Paul, MN, U.S.A.

## ARTICLE INFO

### Article history:

Received 9 December 2016

Initial acceptance 23 January 2017

Final acceptance 7 July 2017

MS. number: A16-01062R

### Keywords:

avifauna  
brood parasitism  
comparative analysis  
cooperative breeding  
phylogeny

There has been great interest in how complex social behaviours such as cooperative breeding evolve and are maintained; however, it is still unclear what exact phenomena trigger the transition to cooperative breeding. Recent work in birds has suggested a number of factors associated with cooperative breeding, including environmental uncertainty and brood parasitism. One recent study found a correlation between brood parasitism and cooperative breeding, but it examined this relationship from a geographically restricted perspective. We investigated evolutionary correlations between brood parasitism and cooperative breeding at a global scale, including nearly half of all bird species and brood parasites. At a global level, we found a strong positive correlation between cooperative breeding and brood parasitism. However, when partitioned regionally, we found that the global pattern was driven exclusively by relationships within Africa and Australia, suggesting that any causal relationship in the transition to cooperative breeding is idiosyncratic. In addition, we found that even where a correlation was supported, transition rates between states were more consistent with cooperative breeding attracting brood parasitism, rather than brood parasites driving the evolution of cooperative breeding, weakening any hypothesized causal connection.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Sociality has arisen many times among animals, likely driven by an array of forces ranging from predation risk (Hamilton, 1971) to foraging efficiency (Brown & Brown, 1996) to environmental unpredictability (Rubenstein & Lovette, 2007). In particular, cooperative breeding, where adults work to help raise offspring not their own, has generated considerable interest since its discovery in birds (Drobnik, Wagner, Mouroucq, & Griesser, 2015; Koenig & Dickinson, 2004; Skutch, 1935; Stacey & Koenig, 1990), in part due to controversy regarding the importance of kin selection in its evolution (e.g. Emlen & Wrege, 1989; Jamieson, 1989). Although the importance of kinship in cooperative breeding now seems clear (e.g. Cornwallis, West, Davis, & Griffin, 2010; Riehl, 2013), the proximate biotic and abiotic factors selecting for it remain controversial. Comparative studies have even found differing, sometimes contradictory factors favouring the evolution of cooperative breeding (e.g. stable environments: Arnold & Owens, 1999; unpredictable environments: Rubenstein & Lovette, 2007).

The evolution of cooperative breeding can be split into at least three major evolutionary questions. First, what preconditions are necessary for the evolution of cooperative breeding? Second, what are the triggers driving pair-living bird species to live in cooperative groups? Third, what are the factors that maintain cooperative behaviours? Ecological triggers, combined with any necessary, historically contingent preconditions (e.g. a monogamous mating system: Cornwallis et al., 2010), drive the formation of cooperative groups and may contribute to their long-term maintenance. Studies investigating ecological drivers of cooperative breeding in individual bird species have produced a number of viable hypotheses, ranging from abiotic factors such as environmental uncertainty to biotic factors like predation (Hatchwell, 2009; Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2004; Riehl, 2013). These and similar studies, while illuminating, could be idiosyncratic to their focal species and not reflect broader trends in the evolution of cooperative breeding; to discern these broader evolutionary trends a comparative approach is needed. Progress in this direction has been made recently with the use of comparative and modelling approaches that have tested a number of novel hypotheses about the factors that could act as triggers for the formation of cooperative groups. To date, most of these studies have focused on abiotic factors, such as seasonality and predictability of the environment

\* Correspondence: M. T. Wells, Department of Ecology, Evolution and Behavior, University of Minnesota, St Paul, MN 55108, U.S.A.

E-mail address: [wells306@umn.edu](mailto:wells306@umn.edu) (M. T. Wells).

<sup>1</sup> E-mail address: [barke042@umn.edu](mailto:barke042@umn.edu) (F. K. Barker).

(Griesser, Drobniak, Nakagawa, & Botero, 2017; Jetz & Rubenstein, 2011; Rubenstein, 2011).

By contrast, one recent study suggested that the evolution of group formation could be driven by a biotic factor, namely brood parasitism (Feeney et al., 2013). Brood parasites are species of birds that lay eggs in the nests of other species, which then raise them, generally at a fitness cost to other young in the nest and the adults attending them. There have been at least seven independent transitions to brood parasitism in birds, and these radiations have occurred across divergent taxa (Davies, 2000). Brood parasites are known to have profound impacts on the evolution of their hosts (see Soler, 2014; for a recent review), but previous work (Poiani & Elgar, 1994) failed to find support for their impact on host social systems. Using two comparative approaches, Feeney et al. (2013) found a correlation between cooperative breeding and brood parasitism in sub-Saharan Africa and Australia. In addition, they found experimentally that superb fairy wrens, *Malurus cyaneus*, were more effective at repelling brood parasites when in large groups, translating into higher reproductive success for all individuals in the group. These findings suggest that brood parasitism might trigger the formation of social groups, and could drive the transition to cooperative breeding on a background of historically contingent factors such as high within-group relatedness. Alternatively, these results could be a noncausal epiphenomenon of cooperative breeding. In this scenario, brood parasites would be attracted to already cooperatively breeding species, either because larger groups are more easily detected, or because brood parasites have a preference for cooperative breeders due to the additional care their offspring might receive (Poiani & Elgar, 1994).

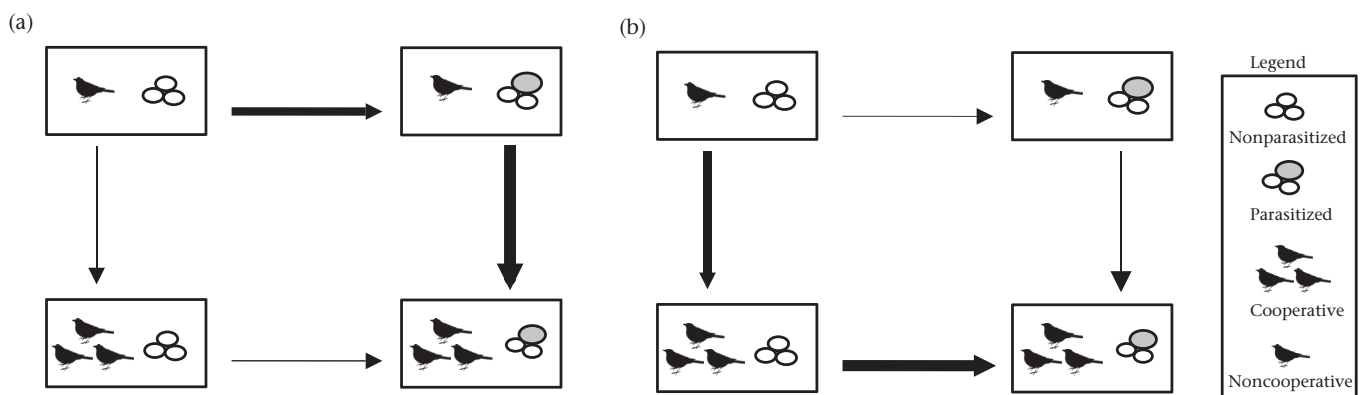
This study attempts to address whether the correlation between cooperative breeding and brood parasitism is a global phenomenon, and if the pattern of inferred transitions between cooperative, noncooperative, parasitized and nonparasitized states support the hypothesis that brood parasitism triggers group formation in cooperative breeders. Portions of Africa and Australia share a number of distinct conditions including strong variation in precipitation both within and among years (Jetz & Rubenstein, 2011) that could drive both cooperative breeding and brood parasitism. Consequently, analysing areas with distinct climatic regimes could help clarify whether brood parasitism is indeed a trigger or merely a correlated response. Also of interest is the phylogenetic composition of the brood parasitic fauna. For instance, there are four independent lineages of brood parasites in Africa (Viduidae, Indicatoridae, and both Cuculinae and Phaenicophaeinae lineages of cuckoos; Aragon, Møller, Soler, & Soler, 1999), and three in the

Neotropics (*Molothrus*, the Neomorphinae lineage of cuckoos, and *Heteronetta atricapilla*). Conversely, Australian parasites are exclusively from the Cuculinae lineage of cuckoos, and North America only harbours members of the genus *Molothrus*. Consistent correlation of brood parasitism with cooperative breeding despite varying pools of parasites would strengthen any causal link between the two. Finally, we expect that if brood parasitism is a global driver of cooperative group formation, then inferred transition rates should be highest for transitions from 'noncooperative and nonparasitized' to 'cooperative and parasitized' by transitioning first to parasitized and only subsequently transitioning to cooperative breeding. By contrast, if the dependency is instead due to brood parasites' attraction to cooperative breeders, transition rates should be equivocal for transitions to cooperative breeding, and the most frequent transition should be to brood parasitism when cooperative breeding is already present (Fig. 1).

## METHODS

### Global Analysis

Cooperative breeding encompasses a number of different social systems, and it is probable that sociality across birds is driven by several distinct mechanisms that are only superficially similar; however, the majority of avian cooperative breeders appear to have kin-based sociality (Riehl, 2013). Unfortunately, the dearth of detailed social system information for most bird species necessitates a broad social/nonsocial categorization. This categorization will necessarily dilute any correlations that are specific to a particular social system (e.g. kin-based groups), but this effect should be neutral with respect to the hypotheses under test. Consequently, we coded breeding system as a discrete, binary trait (either cooperative or noncooperative). We extracted avian breeding system information from Cockburn (2006), with species-specific modifications suggested by Ligon and Burt (2004). While Cockburn attempted to infer the breeding systems in species without explicit study, we included only species with known breeding systems. In addition, we conservatively coded all species with breeding systems listed as 'occasionally cooperative' as noncooperative: in preliminary runs, recoding these categories as 'cooperative' had no effect on the outcome of the analysis (not shown; Griesser & Suzuki, 2016). Finally, several species (e.g. dunnocks, *Prunella modularis*, and carrion crows, *Corvus corone*) have been documented to have substantial intraspecific and interpopulational variation in the propensity to breed



**Figure 1.** Evolutionary transition rates between cooperative breeding and brood parasitism states from an initial state of noncooperative and nonparasitized to an end state of cooperative breeding and parasitized under the hypotheses that (a) brood parasitism drives the evolution of cooperative breeding and (b) brood parasitism is a result of cooperative breeding groups. Each possible state is shown as a box, and directions of transitions between states are indicated with arrows. The weight of the values indicates the transition rate among states, with higher rates of transitions indicated by a heavier line. Reverse transitions are omitted here for clarity.

Download English Version:

<https://daneshyari.com/en/article/5538312>

Download Persian Version:

<https://daneshyari.com/article/5538312>

[Daneshyari.com](https://daneshyari.com)