

Testing for Demographic and Ecological Forces as Drivers of the Evolution of
Cooperative Breeding in Birds

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Dedication

To my parents and sister, who put up with all sorts of strange stuff in the freezer and garage growing up; to my wife, who deals with the same problem now; and to Jim Robertson, who got me a start in birds.

Abstract

Understanding the evolution of social systems, such as cooperative breeding, has been of major interest to biologists. Comparative work has identified several selective factors favoring sociality that receive significant support in global datasets. In this dissertation, I tested the importance of two of these hypothesized drivers independently, and performed the first comparative analyses of multiple potential drivers of cooperative breeding. First, I investigated the relationship between cooperative breeding and brood parasitism at a global and regional scale. I found a strong correlation between the two that may be due to brood parasites being attracted to cooperative breeders rather than by parasites driving the evolution of sociality, as previously supposed. Second, I tested the relationship between promiscuity and social system, using relative testis size as measured from museum specimens as a proxy for mating system. This greatly increased the sample size (by an order of magnitude) over genetic measures of promiscuity and eliminated a strong bias towards data on species from the northern hemisphere. While there were some discrepancies among analyses, I found that cooperative breeding and relative testis size exhibited the negative association expected under indirect benefits models of the evolution of cooperative breeding, despite my less biased and much larger sample of species. Finally, I combined five factors previously suggested to be important in the evolution of cooperative breeding into a single comparative analysis to determine the relative importance and interactions among them. Correlations between cooperative breeding and these predictors were highly dependent on the phylogenetic tree and choice of analysis, but favored a positive association with brood parasitism overall with little

support for interactions. I make recommendations for ways forward toward better understand the evolution of cooperative breeding in a comparative framework.

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INTRODUCTION

TESTING FOR DEMOGRAPHIC AND ECOLOGICAL FORCES AS DRIVERS OF THE EVOLUTION OF COOPERATIVE BREEDING IN BIRDS

Animals vary dramatically in the frequency, duration and types of interactions they have with conspecifics. At one extreme, individuals can interact only in order to reproduce, and have no other non-antagonistic interactions with others. At the other, individuals spend their entire lives in close contact with conspecifics and rarely are found alone. These two extremes affect every aspect of the individuals' life histories, from how quickly individuals mature to how their immune system is regulated. Indeed, shifts to highly social group living have been suggested to be a major evolutionary transition of life on earth, of similar profundity to the evolution of multicellularity. Therefore understanding the evolutionary shift to social living is of considerable interest to biologists. This shift to social living reaches its apogee in eusocial organisms, which exhibit a full reproductive division of labor and in which the majority of individuals in a social group are sterile. However, there is a large range of highly social animals that exhibit different levels of social behavior and different levels of reproductive divisions of labor. This includes organisms such as cooperative breeders, in which some individuals of reproductive age help other individuals in their social group raise offspring. This social system was first described in birds (Skutch 1935) and has since been recognized in a large number of taxa including insects, fish, and mammals—most recently proposed as an aspect of human sociality (Solomon and French 1997; Hogendoorn and Zammit 2001; Hrdy 2007; Wong and Balshine 2011). The interest in social behavior is enduring in part

because of the difficulty in understanding how it evolved. Eusocial species in particular have undergone radical changes to behavior and morphology since the evolution of sociality, making it particularly frustrating to attempt to reconstruct the origins of this system. Cooperative breeding may offer richer opportunities to understand the origins of sociality, as all mature individuals are reproductively capable and tend to have less stable social groups than eusocial animals. Most hypotheses generated to explain cooperative breeding have focused on analysis of lower-level demographics of single populations. This gives strong insight for conditions maintaining sociality at a local scale, but may not be valid across species ranges or among species.

Use of a multi-species comparative framework may be a more powerful approach for understanding the most general determinants of cooperation. An approach using a robust phylogeny, combined with either direct measures or proxies for potential drivers for cooperative breeding provides critical tests of the many hypotheses put forward to explain the evolution cooperative breeding. Indeed, recent studies, especially those focusing on cooperative breeding in birds, seem to have made significant progress. However, these studies are hobbled by several significant drawbacks. First, until recently, there was no species-level phylogeny for most large clades. This has recently changed as new techniques are being used to generate full, species-level phylogenies, using robust but incomplete phylogenies and random grafting techniques for unsampled taxa. Second, sample size is limited in some of these studies due to lack of or significant biases in the data needed to test the traits in question. Finally, and potentially most importantly, all current hypotheses have been studied in isolation, and the relative contributions or interactions of each hypothesized driver are unstudied.

This work attempts to address the shortcomings of current comparative work in cooperative breeding, and to provide a fuller picture of the drivers of the evolution of cooperative breeding in three major phases. In Chapter 1, I used comparative techniques on a global dataset of birds in order to determine if and how cooperative breeding is influenced by a potential biological predictor: brood parasitism. Brood parasites appear to frequently parasitize many cooperative breeders, and this has been hypothesized to provide a selective force to promote cooperative breeding through selection for greater group size, which in turn makes nest defense against parasitism more effective (Feeney et al., 2013). In Chapter 2, I attempt to determine if monogamy promotes the evolution of cooperative breeding, addressing the issue of small sample size from genetic measures of promiscuity by using a proxy for promiscuity, relative testes size measured from museum specimens. Previous work has used direct measures of promiscuity, which while accurate are only available for a small number of species and are biased to specific geographic areas (i.e. the north temperate zone; Cornwallis, et al., 2010). Using testis size as an effective proxy for promiscuity allows generalization of comparative findings to a much larger range of species and environments. Finally in Chapter 3, I use a mixture of proxies and new analytic methods to determine the relative importance of and potential interactions among several hypothesized drivers of cooperative breeding. By determining the relative importance of these factors, we can clarify how these factors may interact with one another in causing the evolution of cooperative breeding. In addition, while these hypotheses have all received significant support in individual comparative analyses, their relative contributions to the evolution of cooperative breeding may have been limited by or confounded with other concomitant changes, which can only be determined

by an integrated analysis. In all of these approaches I take advantage of new species-level phylogenetic trees for birds (Jetz et al. 2012), and report on evaluations of their utility for use in large comparative studies.

CHAPTER 1

BIG GROUPS ATTRACT BAD EGGS: THE COEVOLUTION OF COOPERATIVE BREEDING AND BROOD PARASITISM

There has been great interest in how complex social behaviors, such as cooperative breeding, evolve and are maintained. However, it is still unclear what exactly sparks the transition to group living. Recent work in birds has suggested a number of candidates for this change including environmental uncertainty and brood parasitism. Brood parasites are argued to precipitate group formation by selecting for group-coordinated parasite defense. One recent study found a correlation between brood parasitism and cooperative breeding, but examined this relationship from a geographically restricted perspective. We investigated evolutionary correlations between brood parasitism and cooperative breeding at a global scale, including nearly all bird species. At a global level, we found a strong positive correlation between cooperative breeding and brood parasitism, as found previously for specific continents. However, when we investigated our findings regionally we found that the global pattern is driven exclusively by relationships within Africa and Australia, suggesting a more complex causal relationship in the transition to cooperative breeding. We discuss possible explanations for contrasting global and regional results.

INTRODUCTION

Despite a century and a half of work since Darwin's publication of the Origin of Species (1859), the proximate and ultimate drivers of the evolution of complex social groups remain obscure. Although many hypotheses have been put forward and tested, exactly what ecological, demographic and behavioral forces shape the evolution of cooperative, often seemingly altruistic, behaviors is still largely unresolved in many groups, and there may be no general explanation.

Cooperative breeding, in which one or more adults help a pair of individuals raise offspring not their own (Skutch 1935), has been fertile ground for understanding these forces (Hatchwell and Komdeur 2000; Clutton-Brock 2002; Koenig and Dickinson 2004; Hill and Hurtado 2009). Because non-breeding adults are physically capable of reproducing and are not morphologically distinct (e.g. no reproductive specialization or sterile castes) from breeding individuals, they allow the study of factors that influence the evolution of complex sociality at a stage where driving factors may still be important, rather than attempting to reconstruct ancient events well after the transition to obligate sociality has occurred (Cardinal and Danforth 2011). Indeed, even within cooperatively-breeding species there are strong differences in the propensity of individuals to cooperate (Koenig and Stacey 1990; Komdeur et al. 1995). While cooperative breeding has generated considerable interest since its discovery (Skutch 1935; Stacey and Koenig 1990; Koenig and Dickinson 2004), clear global explanations for how it evolves have proven elusive. Early comparative studies found differing, sometimes-contradictory factors favoring the evolution of cooperative breeding (e.g. stable environments vs.

unpredictable environments, Arnold and Owens 199; Rubenstein and Lovette 2007))

Studies on individual species, many monumental in scope, have produced few conclusions that seem valid at the global level. For example, *Malurus* wrens have been extensively studied as a model of cooperative breeding. However, they are unusual in a number of life-history traits that make the generalization of findings from this genus across all birds—let alone all vertebrates—problematic. For instance, while most cooperative breeders seem to be less promiscuous than non-cooperative birds (Cornwallis et al. 2010), *Malurus* have some of the highest levels of promiscuity recorded for any bird species (Mulder et al. 1994). This difference may indicate that *Malurus*, while convergent with other cooperative breeders in social structure, experiences a wholly different selective regime than the majority of cooperatively breeding birds.

One issue is that 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? Included in this list are factors that influence relatedness among potential group members (Cornwallis et al. 2010), peculiarities in diet that make grouping more or less possible (Heinsohn 1991), or even the simple ability to tolerate conspecifics in close proximity (Lin and Michener 1972). Second, what is the actual trigger shifting pair-living species to live in groups? This shift, when combined with the necessary historical contingencies, drives the formation of cooperative groups. Due to the potentially ephemeral nature of this second transition, and the myriad of potential triggers, this stage has not been well studied from a comparative perspective. However, in the last five years, the implementation of sophisticated comparative and modeling techniques have generated a number of novel hypotheses about the factors that

could act as a trigger for the formation of cooperative groups. Most focus on abiotic or ecological factors, such as predictability of the environment (Jetz and Rubenstein 2011; Rubenstein 2011), or the use of costly, defensible nest structures (Nowak et al. 2010). A final question is, what are the factors that maintain cooperative behaviors, especially in the face of invasion by non-helping cheaters? Considerable theoretical and empirical effort has been applied to solving this question, including investigations using game theoretical approaches (Trivers 1971; Stephens et al. 2002), reciprocal altruism (Wilkinson 1984), and kin selection (Hamilton 1964).

One recent study has suggested that the evolution of group formation could be driven by biotic factors, namely brood parasites (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). Using both comparative and faunal approaches, Feeney et al. found a strong correlation between cooperative breeding and brood parasitism in sub-Saharan Africa and Australia. In addition, they found experimentally that superb fairy wrens (*Malarus 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 may act as a trigger for the formation of social groups and, in the presence of historical contingencies such as high relatedness, could be a driver of the transition to cooperative breeding. Analogues of protection from brood parasitism are also found in other taxa (e.g. protection from predators focusing on immature animals Judd 1998; Gilchrist 2004), and

could make offspring defense in general a universal driver of cooperative breeding behaviors.

However, it is unclear if these results hold across all birds. The Feeney et al. (2013) study did not test this correlation on a global scale, focusing only on southern Africa and Australia. These regions, especially sub-Saharan Africa, have a number of distinct ecological conditions including strong variation in precipitation both within and among years (Jetz and Rubenstein 2011), that could be driving both cooperative breeding and brood parasitism. Looking at areas where this is not the case could help clarify if brood parasitism is indeed a driver or merely byproduct of some underlying mechanism. Also important 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 the *Cuculinae* and *Phaenicophaeinae* lineages of cuckoos; Aragon et al. 1999), and three in the Neotropics (*Molothrus*, the *Neomorphinae* lineage of cuckoos, and *Heteronetta atricapilla*). Conversely, Australia is only represented by the *Cuculinae* lineage of cuckoos and North America only contains members of the *Molothrus* lineage. Differences in the diversity of these assemblages could be important for the number of species parasitized and the occurrence of coevolution between cooperative breeders and brood parasites.

In addition, Poiani and Elgar (1994) posited several alternative hypotheses explaining the correlation between cooperative breeding and brood parasitism. In particular, they suggested that brood parasites might be attracted to cooperative breeders and preferentially parasitize them. They suggested two non-mutually exclusive mechanisms for why this may occur: ease of detection and strategic parasitism. Brood

parasites may parasitize cooperative breeders simply because there is more activity near the nest, making it more detectable. Alternately, they could parasitize cooperative breeders strategically in order to maximize the condition of their offspring by taking advantage of the superior care or protection provided by larger groups. The analyses reported by Feeney et al. (2013) do not provide information about the directionality of the parasitism/cooperative breeding relationship. While the behavioral experiment appears to support the hypothesis that cooperative breeding is being driven in part by fitness benefits resulting from protection from brood parasites, single species studies could be misleading, as discussed above. By examining the inferred directionality of trait evolution, we may better understand the overall dynamics of the interactions between parasitism and cooperative breeding over evolutionary time.

This study attempts to address whether the dependency between cooperative breeding and brood parasitism is a global phenomenon, and if the pattern of inferred state transitions support the hypothesis that brood parasitism triggers the precipitation of group formation in cooperative breeders. We expect dependencies will be most likely to occur in tropical and subtropical regions where there is the greatest concentration of cooperative breeders. We also expect that if this hypothesis is supported, inferred transition rates will be highest for transitions from “non-cooperative and non-parasitized” to “cooperative and parasitized” by transitioning first to parasitized and only then transitioning to cooperative breeding. By contrast, the dependency may instead be due to brood parasites’ attraction to cooperative breeders, either due to ease of locating nests from more activity around them, or due to strategic decisions to parasitize larger groups, which should have a higher capacity for feeding parasite nestlings and in turn improve

the survival and fledging condition of offspring. If this is the case, transition rates should be equivocal for transitions to cooperative breeding, and the strongest transition should be transitions to brood parasitism when cooperative breeding is already present.

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 dearth of detailed social system information for most species necessitates a broad social/non-social categorization. Consequently, breeding system was coded as a discrete, binary trait (either cooperative or non-cooperative). 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 system in species without records, we excluded all species with unknown breeding systems in order to minimize potential biases. In addition, we conservatively coded all species with breeding systems listed as “occasionally” as non-cooperative. In preliminary runs, recoding these categories to “cooperative” had no effect on the outcome of the analysis. The resulting dataset comprised 4997 species, containing 500 cooperative breeders.

Brood parasite host records for all obligate parasitic lineages (*Vidua* indigobirds and *Anomalospiza* finches, Viduidae; *Molothrus* cowbirds, Icteridae; *Indicator* honeyguides, Indicatoridae; subfamily Cuculinae and genera *Dromococcyx*, *Tapera*,

Clamator of the cuckoos, Cuculiformes; and *Heteronetta* ducks, Anatidae) were obtained from Lowther (2013), and this compendium of records was cross-checked with source materials before use. Due to the tendency of *Molothrus* to lay eggs promiscuously in the nests of unsuitable hosts, we excluded all host species that had fewer than ten observations of parasitism recorded. Species were coded for a binary trait indicating their hosting of at least one brood parasite species. This coding does not capture how likely a given host is to be parasitized, regional variations in parasitism, or if multiple brood parasite species use the same host species.

To investigate the correlations among these traits, we used a subset of 1000 stage II trees from the Jetz et al. (2012) phylogeny, for each of two high-level topologies previously hypothesized by Hackett et al. (2008) and Ericson et al. (2006) (“Hackett Backbone” and “Ericson Backbone”, respectively). While the methods used to construct these trees have been debated (e.g. Ricklefs and Pagel 2012; Rabosky, in press), it is currently the best species level phylogeny for bird species available. Maximum clade consensus (MCC) trees for both backbones were constructed using TreeAnnotator v1.8.0 (<http://beast.bio.ed.ac.uk/TreeAnnotator>) with default options. This procedure results in trees with negative branch lengths. To correct for this artifact, negative branches were reflected and downstream branches rescaled to be ultrametric using a script in R (Barker et al. 2015).

Cooperative breeding and brood parasite data were analyzed for correlated evolution using the “discrete” function of *BayesTraits* v2.0, recompiled to handle large trees (Pagel and Meade 2006; Meade pers. comm.). The “discrete” function tests if two binary traits are correlated by comparing the fit of continuous-time Markov models: a

first (“independent”) where the two traits are allowed to evolve independently, and a second (“dependent”) where the transition of one trait is dependent on the value of the other (Pagel and Meade 2006). Bayesian Markov-chain Monte Carlo (MCMC) analyses were performed. We focused on Bayesian analysis because of the ease of measuring and interpreting model fit and transitions among states within models. Based on results from a preliminary maximum likelihood analysis of the data using the Maximum Clade Credibility (MCC) trees, we chose a uniform prior between 0 and 1 for all parameters. Chains were mixed using the “autotune” function, which keeps acceptance rates at approximately 30%. To further test the hypothesis that cooperative breeding evolves in response to brood parasites, we constrained the rates of transition from solitary to cooperative breeding under conditions of both brood parasitism and lack of parasitism to be equal using the “restrict” function in *BayesTraits*. Chains were sampled every 1000 generations, and runs were monitored and run length extended until an adequate sample size was obtained for all parameters. We used *Tracer* v1.5 (<http://beast.bio.ed.ac.uk/Tracer>) to evaluate runs for adequate mixing, to determine if effective sample sizes were sufficient (e.g. ≥ 200), and to identify the percentage of early generations to delete prior to analysis (burn-in). *Tracer* was also used to calculate the \log_{10} Bayes factors between models, using 1000 bootstrap replicates to calculate harmonic mean likelihoods, as well as to calculate the mean values and credibility intervals for all parameters.

Regional and Taxon-Specific Analyses

Geographic regions vary with respect to the composition of both cooperative

breeders and of brood parasites (e.g. tropical versus temperate areas of the world). By analyzing these regional differences, we can determine if global patterns obscure the effects of regional variation or vice versa. To address this, we divided the global dataset into seven distinct biogeographic regions using biogeographic information in Cockburn (2006): Nearctic (North America to Northern Mexico), Palearctic (northern Eurasia), Neotropical (Southern Mexico, Central America and South America), Africa, Indomalaya (Indian Subcontinent, Southeast Asia and Malay Archipelago to Wallace's Line), Australia (including New Guinea and New Zealand), and Holarctic (both Eurasia and North America). Regional datasets varied in size from 113 to 1358 species (Holarctic and Neotropical, respectively, Table 1.1). Species belonging to two or more regions (coded as "widespread", n=176) were omitted from the analysis. We created regional phylogenetic trees by subsampling the global MCC trees on both backbones. Regional analyses using *BayesTraits* were performed as for the global analysis. To further test the hypothesis that cooperative breeding in Australia and Africa evolves in response to brood parasites, we restricted the rates of transition from solitary to cooperative breeding under conditions of both brood parasitism and non-brood parasitism to be equal, as with the global dataset. We ran this model under the same conditions for the regional analyses described above.

In addition, due to significant differences in life histories and responses to environmental variation found in previous studies (e.g., Jetz and Rubenstein 2011), we partitioned the global data into passerine and non-passerine groups, and made corresponding subsample trees using both backbones. These data sets were evaluated as above.

RESULTS

Global

Global datasets were run for 25 million generations, with the first 5 million discarded as burn-in for the dependent models, while independent models were run for 15 million generations, with the first 5 million discarded as burn-in. Tests of correlated character evolution between cooperative breeding and brood parasitism at a global scale found a strong dependency between transitions in brood parasitism and cooperative breeding (Table 1.2), rejecting models of independent character evolution. These results were very similar using both the Ericson (Log_{10} Bayes factor= 12.3) and the Hackett (Log_{10} Bayes factor= 12.4) backbone trees.

The inferred transition rates (Figure 1.1) for the pathway hypothesized by Feeney et al. (2013) from a non-cooperative, non-parasitized ancestor (q_{12} , q_{24}) sum to 0.016. The inferred transition rates for the path from a non-cooperative, non-parasitized ancestor through a cooperative intermediate (q_{13} , q_{34}) sum to 0.067, approximately four times higher than the path through a parasitized intermediate. Furthermore, the transition from non-parasitized to parasitized is also higher when cooperative breeding is present ($q_{34}=0.063$) compared to non-cooperative species ($q_{12}=0.007$). Taken together, these results suggest that there is a strong global correlation between brood parasitism and cooperative breeding. However the pattern of transitions suggests that this correlation is driven by evolution from the non-parasitized to the parasitized state when cooperative

breeding is present, rather than the presence of parasitism being associated with the transition from pair breeding to cooperation.

We tested for the importance of a parasitized background in the evolution of cooperative breeding by running an alternate model which restricts transition rates from non-cooperative to cooperative to be equal for both parasitized and non-parasitized backgrounds ($q_{24}=q_{13}$). When compared to the dependent model, the restricted model should fare significantly *worse* than the dependent model if the parasitized background provides a significantly higher rate of transition to cooperative breeding than the non-parasitized background leading to a better model fit. We found that both the Hackett and Ericson backbones showed only modestly better fits in the dependent model (Hackett Log_{10} Bayes factor=1.5, Ericson Log_{10} Bayes factor=0.965), suggesting that the role of parasitism on the evolution of cooperative breeding has, relatively little impact on model fit.

In addition, there were several other interesting patterns. First, inferred transition rates suggest that evolutionary transitions from non-cooperative to cooperative breeding when parasitized ($q_{24}=0.010$) are much less frequent than transitions from non-parasitized to parasitized when cooperative breeding is present ($q_{34}=0.063$). However, transitions *from* the parasitized state when cooperative breeding is present ($q_{43}=0.063$) occur at the same rate as the transition *to* the parasitized state when cooperative breeding is present ($q_{34}=0.063$), suggesting parasitism evolves and is lost at relatively high rates in cooperative breeders. In addition, transitions from non-cooperative to cooperative are higher when parasitism is present ($q_{24}=0.010$) than when parasitism is absent ($q_{13}=0.004$), suggesting that brood parasitism may play a role in cooperative breeding. However, we

find that brood parasites appear to play a stronger role in the transition *from* cooperative breeding ($q_{42}=0.092$) than they do in the transition *to* cooperative breeding ($q_{24}=0.010$).

Regional

Regional datasets were run from 10.5-20.5 million generations, and we discarded the first 0.5 million iterations as a burn-in. When tests of correlated evolution were repeated for each biogeographic region, only Africa and Australia reflected the global correlation between brood parasitism and cooperative breeding (\log_{10} Bayes factors: Africa=13.91, Australia=3.95; Table 1.3). These results were consistent across both the Ericson and Hackett backbone trees (Table 1.4), and suggest that African and Australian regions alone drive the global correlation between cooperative breeding and brood parasitism.

When comparing transition rates of the African, Australian, and the global results (Figure 1.2), there were few similarities common to all three, indicating that these two regions exhibit divergent evolutionary dynamics. Africa tends to have higher values for all transition rates (e.g. global: $q_{34}=0.043$, Africa: $q_{34}=0.525$), but follows the global transition rate pattern closely. Overall, Australian transitions are lower than the global rates (e.g. global: $q_{34}=0.043$, Australia: $q_{34}=0.017$). When comparing Australian transition paths from non-cooperative, non-parasitized to cooperative and parasitized we find that both paths are more equal in the magnitude of their rates (q_{13} , $q_{34}=0.020$; q_{12} , $q_{24}=0.014$) than African and global pathways that favor a secondary transition to brood parasitism (q_{13} , q_{34}) much more than a primary transition (q_{12} , q_{24}).

Evolutionary transitions from non-cooperative to cooperative breeding when brood parasitism is present (q_{24}) were found to be higher than the global rates for both Africa and Australia. This shared rate increase could suggest a mechanism for the correlation. We tested this possibility by restricting the transition to cooperation in both parasitized and non-parasitized backgrounds to a single rate ($q_{24}=q_{13}$), which should produce a significantly worse fit than the full model if the transition from non-cooperative to cooperative is being affected by the presence of brood parasitism. We found that the fit of this model was indistinguishable from the full model for Africa ($\text{Log}_{10}\text{Bayes factor}=-0.256$) (Appendix Table 1.1), while there was a slight positive difference in the models for Australia ($\text{Log}_{10}\text{ Bayes factor}=0.707$) (Appendix Table 1.1), suggesting that the presence of brood parasitism does not affect the evolutionary transition from non-cooperative to cooperative breeding in Africa, but may have a modest effect in Australia.

Overall, the African transitions mirror the global transitions writ large, with transitions being gains and losses of parasites in cooperative breeders ($q_{34}=0.525$, $q_{43}=0.630$), while the Australian transitions are dominated by the loss of brood parasites ($q_{21}=0.029$) and cooperative breeding ($q_{31}=0.062$)

Passerine/Non-Passerine

Passerine and non-passerine dependent and independent models were run for 15.5 million generations with the first 0.5 million generations discarded as a burn-in. Both passerines and non-passerines showed substantial correlation between transitions in brood parasitism and cooperative breeding ($\text{log}_{10}\text{ Bayes factors}$: passerines=3.043, non-

passerines=2.444 (Table 1.5)). Transition rates for passerines were highest with transitions to ($q_{34}=0.788$) and from ($q_{43}=0.748$) brood parasitism when cooperative breeding was present, again suggesting that these transitions are central to the dependency (Figure 1.3). In passerines and non-passerines, transitioning through a cooperatively breeding intermediate before being parasitized (passerines: $q_{13},q_{34}=0.793$, non-passerines: $q_{13},q_{34}=0.084$) was much more likely than transitioning to brood parasitism before cooperative breeding (passerines: $q_{12},q_{24}=0.065$, non-passerines: $q_{12},q_{24}=0.039$), similar to global patterns.

Transitions to cooperative breeding were similar to global levels when brood parasites were both absent ($q_{13}=0.005$) and present ($q_{24}=0.014$). Non-passerines had the highest transition rates from parasitized to non-parasitized against both cooperative and non-cooperative background conditions ($q_{21}=0.201$, $q_{43}=0.357$), suggesting that non-passerines may be especially efficient at combating brood parasites over evolutionary time. Interestingly, while still consistent with global and regional results, the transition rate from non-cooperative to cooperative when brood parasitism is present is over three times higher than the global rates ($q_{24}=0.033$), suggesting brood parasitism may indeed be important in the evolution of cooperative breeding.

DISCUSSION

Global patterns support the attraction of brood parasites as a cause for the correlation between cooperative breeding and brood parasitism

Globally, we found a strong dependence between transitions of brood parasitism and cooperative breeding across birds, as noted previously for regional avifaunas (Feeney et al. 2013). This dependence was strongly supported for both the Ericson and Hackett backbone topologies of our phylogeny, suggesting that our findings are robust to unresolved differences in the phylogeny. Rather than supporting the hypothesis that the presence of brood parasites precipitates group formation through increased effectiveness in defense against brood parasites, suggested by the results of Feeney et al. (2013), our inferred transition rates are consistent with predictions that cooperative breeders are chosen by brood parasites due to ease of locating the nest from increased traffic, or due to greater potential fitness advantages for parasites' offspring due to the greater number of caretakers (Poiani and Elgar 1994). We found that overall, transitions from non-cooperative and non-parasitized to cooperative and parasitized are more than four times faster along a path from non-cooperative to cooperative, followed by a transition from non-parasitized to parasitized (q_{13}, q_{34}), than a path transitioning first to parasitized before transitioning to cooperative breeding (q_{12}, q_{24}). When we re-ran the global dataset while restricting the transitions to cooperative breeding to a single rate ($q_{13}=q_{24}$), we found that the dependent model had a modestly better fit than the restricted model (\log_{10} Bayes Factor=1.0). This suggests that the differences between the parasitized and non-parasitized backgrounds are real and affect the fit of the model. However, compared to the differences between the two routes above, the effects of these transitions appear modest overall. Transitions between parasitized (q_{34}) and non-parasitized (q_{43}) for cooperative breeders appear to be roughly similar ($q_{34}=0.043, q_{43}=0.046$), suggesting that coevolution between cooperative breeders and brood parasites is to some degree in an

equilibrium. By contrast, the single highest transition rate for global models was from cooperative to non-cooperative breeding in the presence of brood parasites ($q_{42}=0.083$), suggesting that over evolutionary time, brood parasites tend to drive the *collapse* of cooperative breeding behaviors, rather than enhance them.

An alternate interpretation of the results is that evolution proceeded from a parasitized, cooperative breeding ancestor with fast losses leading to non-parasitized and non-cooperative descendent lineages. This seems unlikely, as the origins of both cooperative breeding and brood parasitism appear to have occurred a number of times (Friedmann 1955; Edwards and Naeem 1993; Sorenson and Payne 2001; Payne 2005; Cockburn 2006).

No regions other than Africa and Australia demonstrated significant correlations between cooperative breeding and brood parasitism. While these findings are consistent with the findings of Feeney et al., it is surprising that no other regions show the same trend. Consequently, these two areas appear to be driving the global pattern we report here. One caveat for this finding is the relatively poor behavioral and parasitism data at the species level in several of the regional datasets, most prominently Indomalaya and the Neotropics. However, both of these areas still have a substantial number of species, and the Neotropics in particular constitutes the single largest number of species for any region, and both of these regions show weak evidence *against* the dependent model (Table 1.2) (Kass and Raftery 1995).

On transitions to brood parasitism, it is possible that Africa and Australia have more species of brood parasites and therefore higher rates of brood parasitism overall, giving these areas more power. Indeed, African and Australian species have a high

incidence of species that are parasitized (Africa=26%, Australia=27%). However, the Indomalayan biogeographic region has a similar rate of parasitism (24%), but shows no correlation. In addition, the New World *Molothrus* cowbirds are particularly effective at exploiting multiple host species, unlike the more speciose but more specialized cuckoos, and this difference in host specificity is reflected in the Neartic, where over half (53%) of species act as hosts for brood parasites, but again these brood parasites show no correlation with cooperative breeding. While Neotropical species are parasitized at lower rates than species in other tropical areas (16% of species), and therefore may be under sampled, they still constitute a substantial fraction of the species listed.

Correlated evolution in Africa

The dependent model of the African biogeographic region is the most strongly supported of any analysis (Log_{10} Bayes Factor=13.91). It largely follows the global pattern of transition rates, with some minor differences. First, the transition path from non-cooperative and non-parasitized to cooperative and parasitized still favors transitions to cooperative breeding followed by brood parasitism ($q_{13}, q_{34}=0.531$). However, when compared to the path in which the transition to brood parasitism occurs first ($q_{12}, q_{24}=0.022$), the magnitude of the difference is much greater (over 24-fold) than the global transition estimation (over 4-fold). Compared to the global rates, the transition *from* cooperative breeding in the presence of brood parasites is lower ($q_{42}=0.13$), but is still an order of magnitude higher than the opposite transition ($q_{24}=0.014$). In addition, like the global results some of the highest transition rates for Africa are the transitions to and from brood parasitism when cooperative breeding is already present ($q_{43}=0.78, q_{34}=0.66$).

When we restricted transitions to cooperative breeding (q_{13} , q_{24}), we found that this model has the same fit as the dependent model ($\text{Log}_{10}\text{Bayes Factor}=0.097$), suggesting that differences in the rates of transition to cooperative breeding are unaffected by the presence of brood parasitism. Taken together, the regional results for Africa mirror our conclusions for the global analysis: the dependence between cooperative breeding and brood parasitism appears to be due to brood parasites exploiting species that are already cooperatively breeding, rather than brood parasites being present before the transition to cooperative groups.

Two potential explanations for why we observe the pattern of cooperative breeding and brood parasitism in Africa require further testing. First, the correlation we observe could be driven by regional differences in the number and type of brood parasites in the area. Some biogeographic regions may harbor a greater variety of brood parasites, either through novel transitions to brood parasitism, or through invasion by cosmopolitan species. Africa is home to at least two independent transitions to brood parasitism: whydahs and indigobirds (Viduidae; Friedmann 1960; Sorenson and Payne 2001) and *Indicator* honeyguides (Indictoridae; Friedmann 1955). In addition to these two unique radiations, there are at least fourteen species of cuckoo known to inhabit Africa (Payne 2005). The African brood parasites are taxonomically diverse, with representatives from three (Piciformes, Cuculiformes, and Passeriformes) of the only four orders in which brood parasitism has evolved (Davies 2000). Finally, while dating the evolution of brood parasitism is poor, the whydahs and indigobirds at least represent an old (~20 million yrs) transition to parasitism, suggesting that brood parasites have had a long period of time in order to coevolve with hosts (Sorenson and Payne 2001), as well as spread to new hosts.

This is likely true for cuckoos (especially the *Cuculini* radiation; Sorenson et al. 2005), and may be true for honeyguides, as well (Spottiswoode et al. 2011). This combination of factors could cause African brood parasites to be able to use a greater diversity of hosts than in other places, and therefore may be more likely to parasitize cooperative breeders. The Neotropics are also home to three radiations of parasites: the Cowbirds (*Molothrus*), New World Parasitic cuckoos (*Dromococcyx* and *Tapera*), and the *Heteronetta* ducks (Anatidae). However, neither cuckoos nor brood parasitic ducks have undergone significant diversification (cuckoos: 3 species; ducks: 1 species), while the *Molothrus* cowbirds only acquired brood parasitism relatively recently (Powell et al. 2014). Further investigation into the timing and region of origin of brood parasitism is necessary before the importance of brood parasite diversity and age can be assessed.

Second, the correlation between brood parasites and cooperative breeders in Africa may be driven not by interactions between the species per se, but due to underlying ecological conditions that are favorable both to the adoption of cooperative breeding and to brood parasitism. Work by Jetz and Rubenstein (2011) found that environmental uncertainty, especially interannual variation in precipitation (for passerines) and temperature (for non-passerines) was a strong predictor of cooperative breeding in passerines. They concluded that cooperative breeding acts as a bet-hedging strategy for adult offspring, which accrue fitness at a low but predictable rate rather than attempt to breed independently, when a poor rainfall year could end all hope of reproduction. In a similar fashion, brood parasitism could be a similar bet-hedging response to environmental uncertainty. Brood parasites pay little cost for reproduction outside of the physical production of eggs. Costs of a bad season are therefore not borne

by the parent, as long as they survive. In addition, if the evolution of brood parasitism follows the hypothesized mechanism of intraspecific parasitism leading to specialization before generalization (Lanyon 1992), environmental uncertainty could trigger this mechanism by favoring intraspecific brood parasitism. In uncertain environments, laying eggs in neighboring nests could act as a bet-hedging strategy: even if the primary nest doesn't survive, individuals could still gain fitness if nests that were parasitized fledged offspring. Additional research is needed to disentangle how brood parasitism, cooperative breeding and environmental uncertainty may interact.

Correlated evolution in Australia

The Australian biogeographic region differs in several respects from both the global and the African analyses. First, the transition rates for Australia are generally lower in magnitude than the global rates (Figure 1.2) with two exceptions: the shift from cooperative to non-cooperative in the absence of brood parasitism (q_{31}) and the shift from non-cooperative to cooperative in the presence of brood parasitism (q_{24}) are both larger than the global rate. When we restricted the transition to cooperative breeding, we found weak but positive evidence that the restricted model has a worse fit than the dependent model (\log_{10} Bayes Factor=0.797). This indicates that the two transitions to cooperative breeding are different enough to have a positive effect to the overall fit of the model, suggesting that the rate of change to cooperative breeding is different between non-parasitized and parasitized backgrounds. Due to the lack of dated phylogenies for parasitic cuckoos (although see Sorenson et al. (2005) for discussions on *Centropus* and *Couinae*), it is unclear when brood parasites spread to Australia. Further understanding of

the timing of this spread is crucial to determining the potential coevolutionary dynamics between parasite and host and could help us better understand the role of parasitism on the evolution of cooperative breeding. Overall, there is greater evidence in Australia than other regions of the world for brood parasitism influencing the evolution of cooperative groups. However, the pathway to cooperative breeding and brood parasitism is equivocal and still slightly favors a cooperative intermediate ($q_{13}, q_{34}=0.0182$) over a parasitized intermediate ($q_{12}, q_{24}=0.0165$), more consistent with the hypothesis that brood parasitism is driven by cooperative breeding.

Taxonomic variation in global correlation patterns

Both passerines and non-passerines in general follow the global patterns. We found passerines are more than twelve times more likely to shift to cooperative and parasitized by transitioning to cooperative breeding first (q_{13}, q_{34}) than by transitioning to brood parasitism first (q_{12}, q_{24}), while non-passerines are more than twice as likely to transition through a cooperative intermediate. In passerines, the largest inferred transition rate was the shift from non-parasitized to parasitized when cooperative breeding was present (q_{34}) and from parasitized to non-parasitized when cooperative breeding was present (q_{43}). This combination again suggests that brood parasitism is contingent on cooperative breeding, rather than vice-versa. In contrast, the loss of brood parasites in cooperative breeders (q_{43}) was by far the strongest in non-passerines. This pattern is also unique because the transition *to* brood parasitism is generally similar in magnitude in global and regional results, while in non-passerines losses of brood parasitism under cooperative breeding are four times greater. One possible explanation for this is use of

cavity or hole nests by many cooperatively breeding non-passerines (e.g. red-cockaded woodpeckers, Lennartz et al. 1987; green woodhoopoes, Ligon and Ligon 1990; and bee-eaters, Fry 1972). These nests are often limited in supply, either due to high competition for existing spaces, or due to costs of excavation (red-cockaded woodpeckers, Walters et al. 1992; green woodhoopes, Du Plessis 1992), creating a potential for family grouping. The nature of these nest types, with the single small aperture to access the nest, also allows a single bird or a few birds to effectively control the nest entrance. This in turn provides protection from parasitism as long as there is an individual present to occupy the nest or stay near the nest entrance. Larger numbers of individuals in the group could more effectively guard the nest entrance than a single bird or pair of birds. Indeed, there is some evidence that this strategy is effective. In passerine carrion crows (*Corvus corone*), cooperative breeding is effective at deterring cuckoo parasitism because helpers provision the dominant female, removing the need to leave the nest uncovered (Canestrari et al. 2009). Similarly, the use of burrows in some bee lineages is hypothesized to increase social behavior because it allows a few individuals to defend the colony from parasitoids, allowing others to spend more time provisioning (Lin and Michener 1972; Evans 1977).

Losses of cooperative breeding are more common than expected

Transitions from cooperative breeding (q_{31} , q_{24}) were higher than the forward transitions in both parasitized (q_{24}) and non-parasitized backgrounds (q_{31}). This result is surprising, given previous work (e.g., Edwards and Naeem 1993) which concluded that losses of sociality are uncommon. There could be several possible explanations for this pattern. First, the species investigated by Edwards and Naeem are small samples of the

global species pool. These samples could be biased towards groups with unusually low reversals of cooperative breeding, masking how labile cooperative breeding may be. Second, cooperative breeding as commonly defined encompasses a range of social systems, from groups composed of close family members contributing to care of a single nest (e.g. *Campylorhynchus nuchalis* Rabenold, 1985), to complex groups of individuals helping at multiple nests (e.g. starlings, Wilkinson 1982; Keith et al. 2000). The binary designations commonly used (including here) may be too simplistic, and it is possible that the patterns found by Edwards and Naeem may be due to a more homogenous sample of social structures than used here. Splitting taxa using finer-grained methods such as social system type (e.g. nuclear family vs. kin neighborhoods, Hatchwell 2009) may reveal a more complex pattern than the one we found here, with some social systems being especially vulnerable to losses of cooperative breeding while others may be more resilient than expected; however, the data for such a fine-grained analysis are extremely limited.

In the five analyses indicating correlated evolution between brood parasitism and cooperation (global, Africa, Australia, passerine, and non-passerine), the transition to non-cooperative when brood parasitism is present was highest in three analyses (global, Africa and passerines), while the transition to non-cooperative when brood parasitism is absent was highest in the remaining two analyses (non-passerine and Australia). The percent of non-passerines in the Australian datasets (45.9%) and the number of cooperative non-passerines in Australia (18 of 337 non-passerines) do not appear to suggest unusual levels of cooperative non-passerines in this dataset that could explain these shared differences. These two regions merit additional attention to explain this

pattern. One possibility is that cooperative non-passerines and Australian birds are far more limited by environmental variables than they are by brood parasites. For example, several cooperative non-passerine species are cavity nesters, and appear to be limited by these cavities (e.g. red-cockaded woodpeckers, green woodhoopoes, hornbills). If these limitations were suddenly lost, such as changes in fire regimes, rainfall or tree diversity, cooperative breeding might disappear.

While it is unclear what is causing the shifts from cooperative breeding in the absence of brood parasites, we propose the following mechanism for the loss of cooperative breeding in the presence of brood parasites. Cooperative breeders live in a range of social structures, but one of the most common is that of a single breeding pair and their adult offspring being retained on the territory. These adult offspring can achieve breeding status through queuing for inheritance of the breeding position or by dispersing to open breeding positions. Retained offspring are hypothesized to increase their fitness while waiting to disperse either by directly benefitting from living in high-quality territories or through indirect fitness accrued from helping raise siblings (Wiley and Rabenold 1984; Mumme 1992). Heavy brood parasitism could reduce the number of new animals fledged to replace non-breeding adults as they die, disperse or inherit the breeding position, resulting in reduced group size. During this time, larger groups may indeed be more effective at reducing brood parasitism through more effective mobbing (as found by Feeney et al.), but will also be more visible to brood parasites due to a greater disparity in nest visits compared to smaller groups. In addition, nestling brood parasites are effective at manipulating their hosts into providing more care than would be given to their own nestlings (Dearborn 1999; Kilner et al. 1999; Tanaka and Ueda 2005).

If this increase in care is costly to the survival of the group-members (Hoover and Reetz 2006), it could shorten intervals between openings in breeding positions, either through mortality or through retained offspring ousting the weakened dominant members of a group. This combination of greater opportunities for dispersal and lower production of helping offspring would combine to drive a collapse of cooperative breeding.

CONCLUSION

Overall, we argue that strong global correlations between brood parasitism and cooperative breeding mainly support the hypothesis that cooperative breeding serves as an attractant to brood parasites, by contrast with recent evidence that it may evolve in response to parasitism (Feeney et al. 2013). As previously noted (Poiani and Elgar 1994), this may be because of the greater visibility of nests or possibly due to strategic parasitism of cooperative groups to confer higher fitness to progeny raised by large groups. Interestingly, this global correlation appears to be driven by patterns in only two regions: Africa and Australia. Analyses of African birds are consistent with the findings of the global analyses, whereas analyses of correlations within Australia suggest that two paths to cooperative breeding and brood parasitism are roughly equivalent. In addition, separate analyses of passerines and non-passerines indicate that both groups also strongly support the hypothesis that cooperative breeding attracts brood parasites. Interestingly, non-passerines have much higher losses of parasitism in the cooperative background (q_{43}) when compared to gains of parasitism in the same background (q_{34}), unlike passerines, where these transitions are roughly equal. We speculate that the use of nesting cavities by

non-passerines, when combined with cooperative breeding could limit access to the nest for brood parasites.

The complex patterns inferred here warrant further investigation, and open a number of avenues for future study. It is yet to be determined if brood parasites preferentially target cooperative breeders due to ease of locating the nest, or if they are strategically improving the fitness of their young by targeting large groups. In addition, it is unclear why only two geographic regions exhibit a correlation between parasitism and cooperative breeding. Further inquiry into the importance of the diversity and length of coevolution with brood parasites may be fruitful in addressing this question. The use of more complex evolutionary models, especially those that can explicitly take into account how brood parasites and hosts interact and potentially co-speciate with one another through evolutionary time, would be beneficial. Additionally, better species-level studies of interactions between cooperative breeders and brood parasites such as those conducted by Feeney et al. (2013) will be useful in helping to understand the coevolutionary dynamics of cooperative breeding, brood parasitism, and ecological conditions.

Table 1.1— Regional sample sizes.

Biogeographic Region	Number of Species
Africa	1082
Antarctica	48
Australia	732
Holarctic	113
Indomalayan	504
Nearctic	344
Neotropical	1358
Palearctic	642
Widespread	176

Table 1.2— Bayes results of the global analysis. Likelihood measurement includes 95% Confidence interval. K is the Bayes factor for comparison of dependent and independent models (**=very strong evidence; Kass and Raftery 1995).

	Likelihood	Harmonic Mean	log₁₀ K
Ericson Backbone			
Dependent Model	-3517.2 ± 0.13	-3517.68	12.27**
Independent Model	-3545.5 ± 0.08	-3547.21	—
Hackett Backbone			
Dependent Model	-3524 ± 0.12	-3524.7	12.40**
Independent Model	-3552 ± 0.09	-3553.8	—

Table 1.3— Bayes factors (K) for regional analyses on the Hackett backbone tree

(*=**strong evidence**, **=**very strong evidence**; Kass and Raftery 1995). See Table 1.4 for corresponding values on the Ericson backbone for Africa and Australia. All values are for the dependent model.

Region	log₁₀ K
Africa	13.91**
Antarctica	-0.17
Australia	3.95*
Holarctic	-1.46
Indomalayan	-1.57
Nearctic	-1.46
Neotropical	-1.42
Palaearctic	-0.63
Widespread	-1.01

Table 1.4— Model values for Africa and Australia with Hackett and Ericson Backbones.

	Likelihood	Harmonic Mean	log₁₀ K
Africa			
Dependent Ericson	-934.84 ± 0.078	-940.98	11.19
Independent Ericson	-965.62 ± 0.065	-966.42	—
Dependent Hackett	-942.55 ± 0.057	-944.35	13.91
Independent Hackett	-974.58 ± 0.069	-976.02	—
Australia			
Dependent Ericson	-497.86 ± 0.109	-500.01	4.61
Independent Ericson	-507.23 ± 0.073	-508.19	—
Dependent Hackett	-500.39 ± 0.10	-501.53	3.96
Independent Hackett	-509.51 ± 0.063	-510.02	—

Table 1.5— Passerine vs. Non-Passerine distributions.

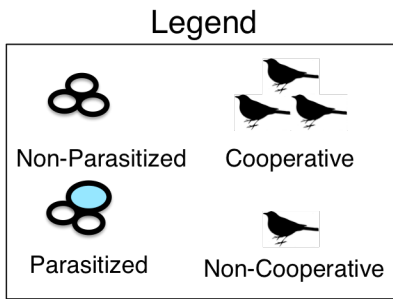
a.

Non-Passerine			
	Likelihood	Harmonic Mean	log₁₀ K
Ericson Backbone			
Dependent Model	-854.546 ± 0.036	-858.461	2.444
Independent Model	-860.174 ± 0.077	-858.402	—
Hackett Backbone			
Dependent Model	-858.23 ± 0.58	-863.222	2.168
Independent Model	-863.22 ± 0.06	-863.72	—

b.

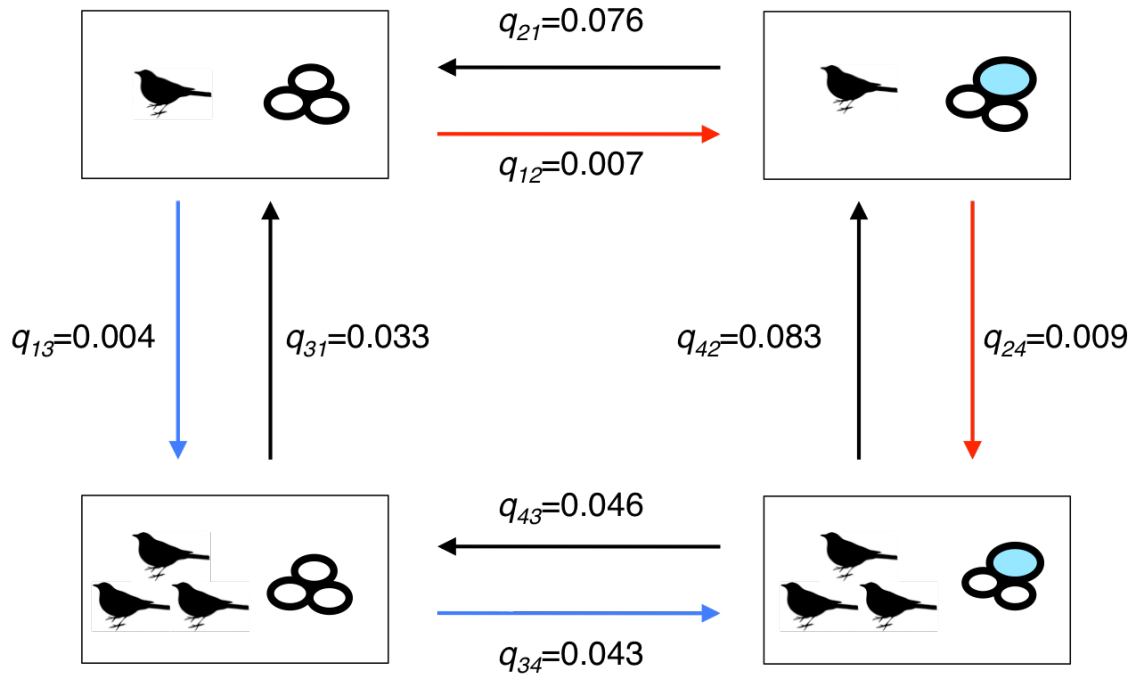
Passerine			
	Likelihood	Harmonic Mean	log₁₀ K
Ericson Backbone			
Dependent Model	-2506.517 ± 0.061	-2508.732	3.043
Independent Model	-2513.525 ± 0.065	-2515.881	—
Hackett Backbone			
Dependent Model	-2518.35 ± 0.08	-2521.23	2.83
Independent Model	-2524.86 ± 0.08	-2526.86	—

Figure 1.1— Inferred global evolutionary transition rates between cooperative breeding and brood parasitism states for the (a.) Hackett backbone and (b.) Ericson backbone trees. Each possible state is shown as a box. Directions of transitions between



states are indicated with arrows. q_{ij} gives the transition rate from i th state to the j th state. Red arrows highlight the transitions hypothesized by Feeney et al (2013). Blue arrows highlight the transitions hypothesized by Poiani and Elgar (1994).

a.



b.

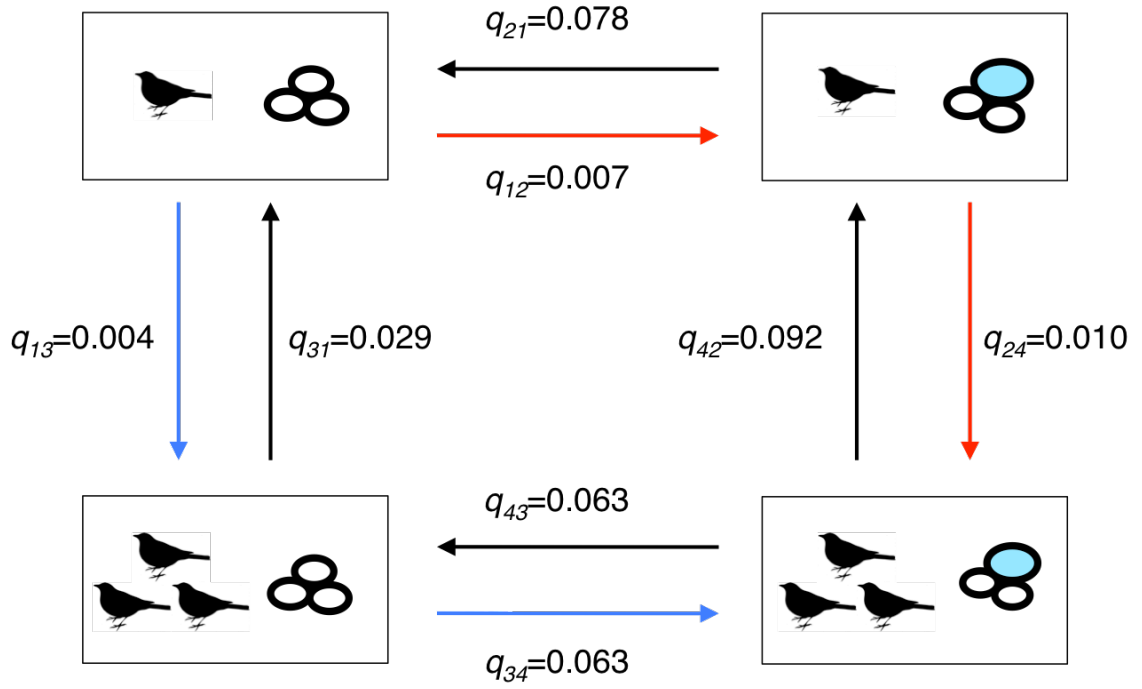
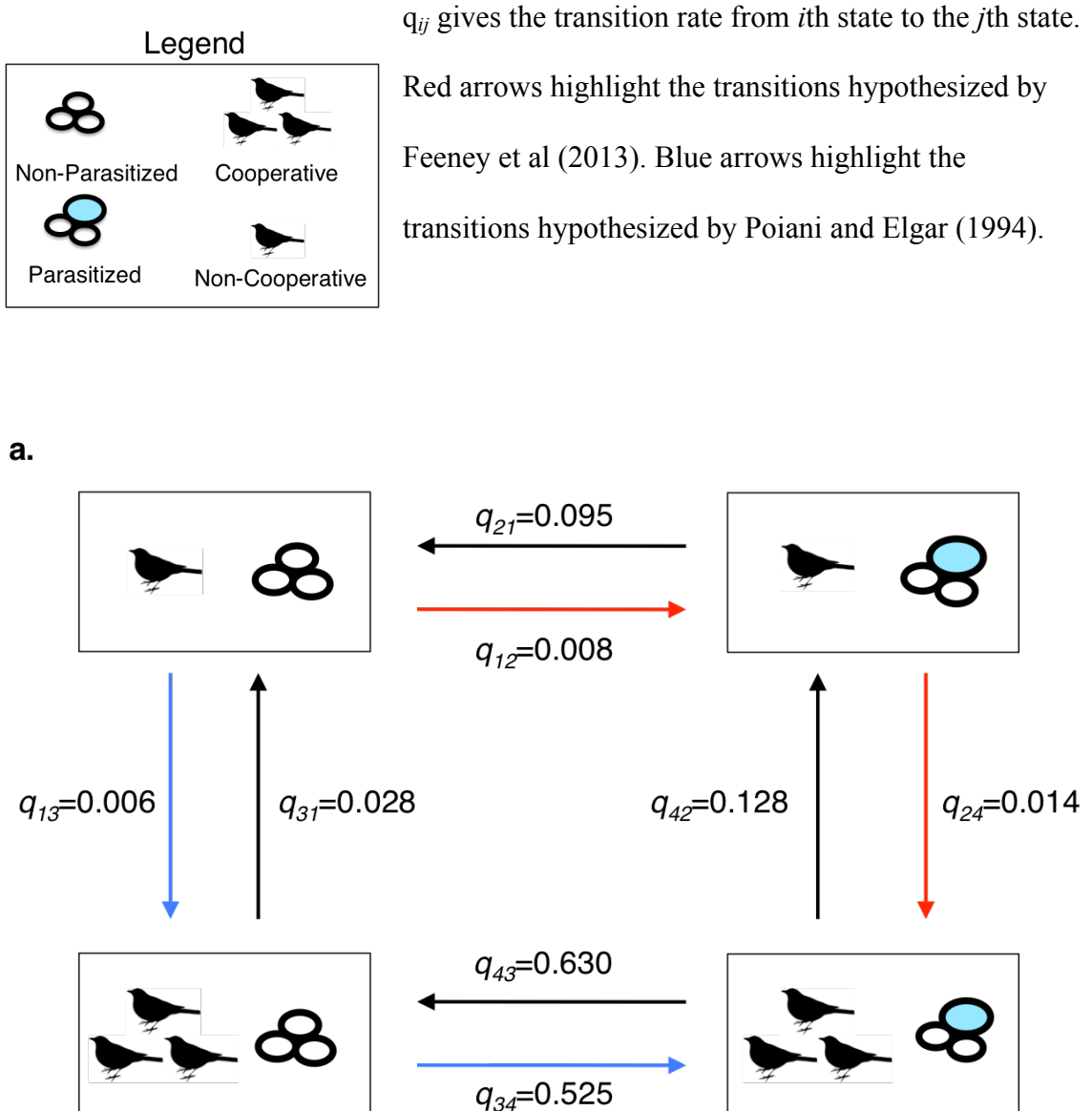


Figure 1.2— Inferred evolutionary transition rates in cooperative breeding and brood parasitism states for (a) African and (b) Australian regions. Each possible state is shown as a box. Directions of transitions between states are indicated with arrows.



b.

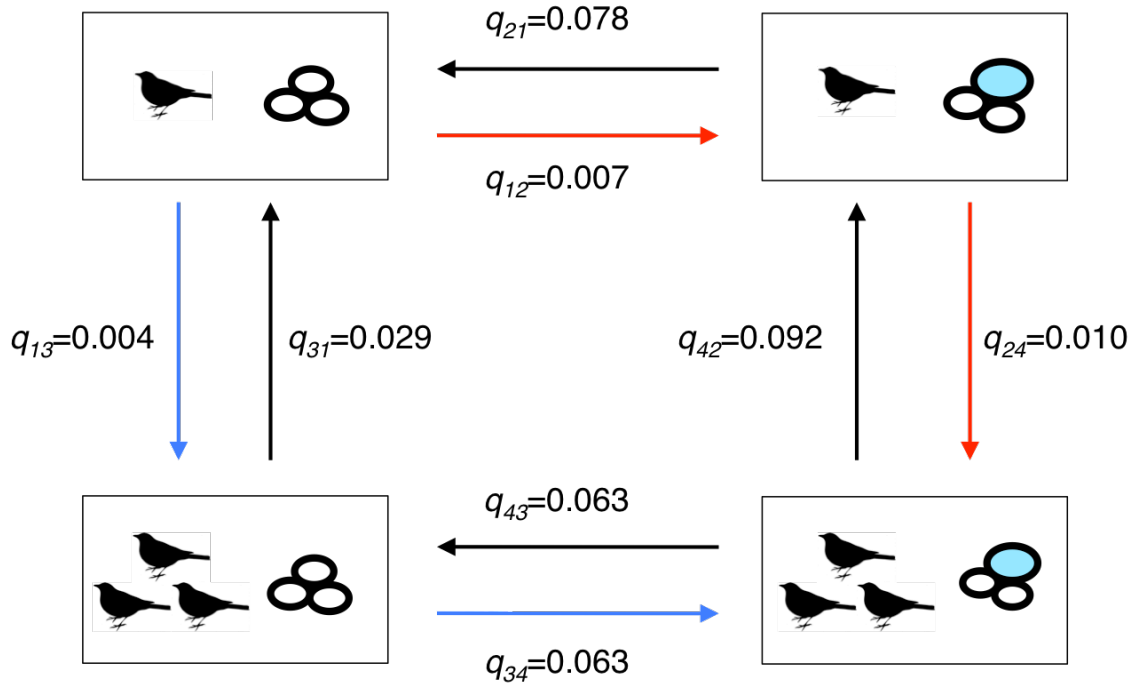
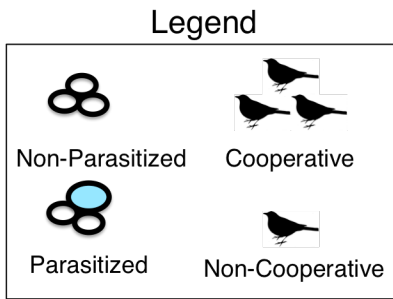


Figure 1.3— Inferred evolutionary transition rates in cooperative breeding and brood parasitism states for (a) Passerines and (b) Non-Passerines. Each possible state is shown as a box. Directions of transitions between states are indicated with arrows. q_{ij}

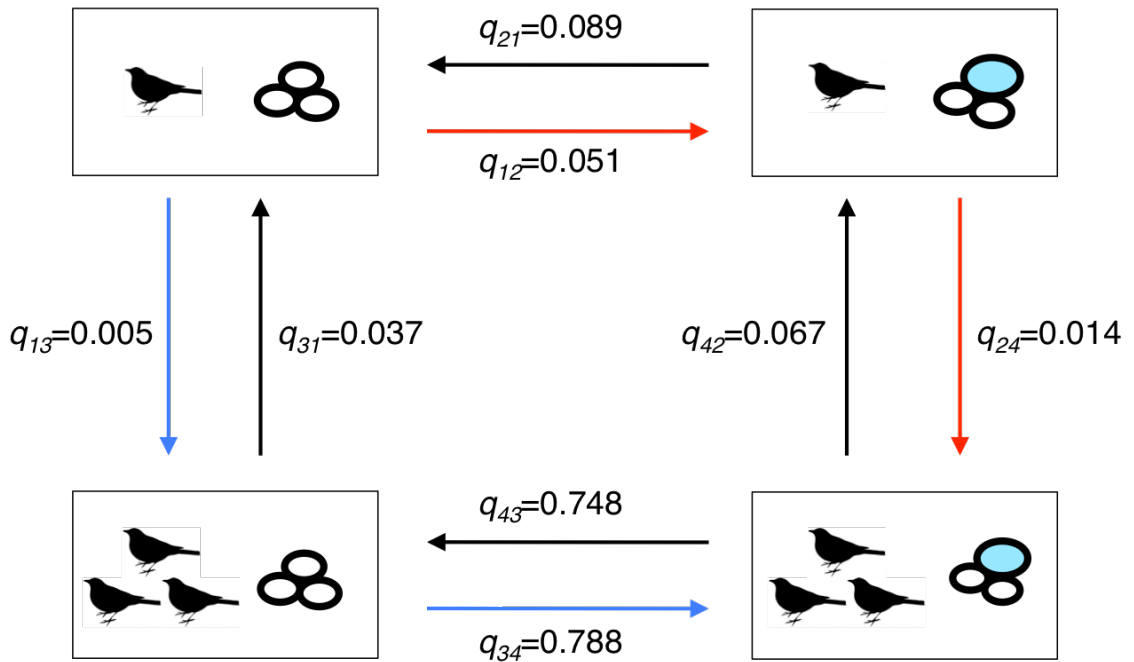


gives the transition rate from i th state to the j th state.

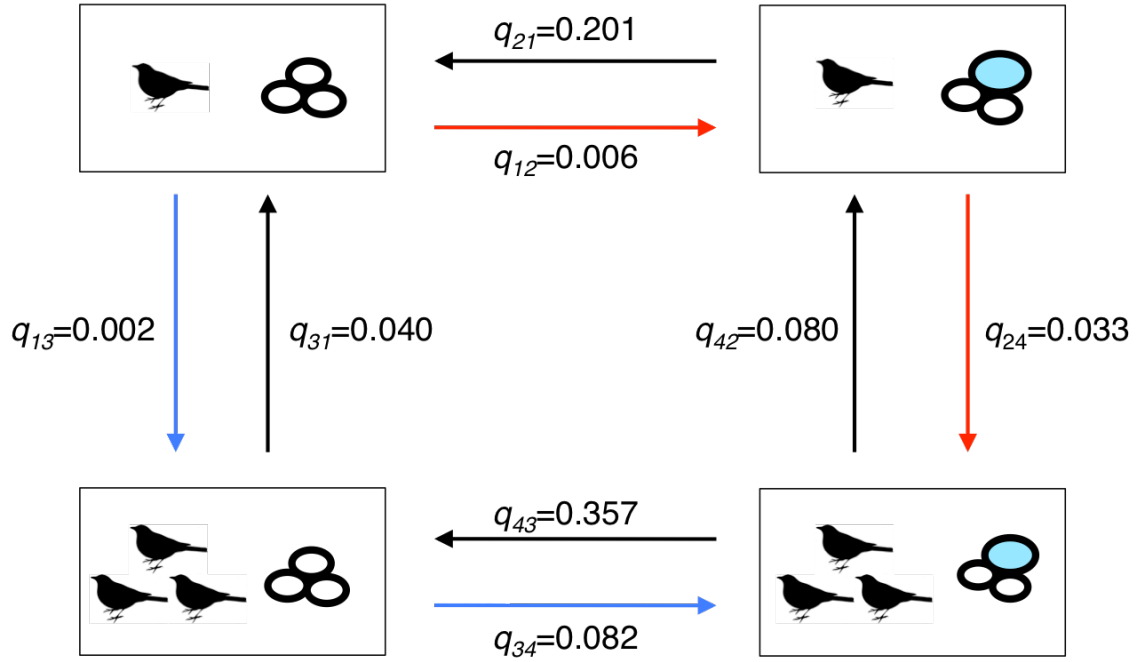
Red arrows highlight the transitions hypothesized by Feeny et al (2013). Blue arrows highlight the

transitions hypothesized by Poiani and Elgar (1994).

a.



b.



CHAPTER 2

ANALYSIS OF RELATIVE TESTIS SIZE FROM A GLOBAL SAMPLE OF BIRDS SUPPORTS AN INDIRECT BENEFITS EXPLANATION FOR THE EVOLUTION OF COOPERATIVE BREEDING

In highly complex animal societies such as those with cooperative breeding, individuals help others often at an apparent loss of fitness because they help others raise young. One hypothesized explanation for this phenomenon is inclusive fitness, where non-breeding individuals accrue fitness by helping other individuals that share their genes. One prediction of this hypothesis is that groups that exhibit cooperative breeding will have offspring highly related to the helping individuals in the group, which would require strong genetic monogamy of the breeding pair. Indeed Cornwallis et al. (2010) found this result using direct measures of promiscuity in birds. However, the use of genetic measures of promiscuity led to a sample of species biased to the north and away from the more speciose tropics. We validated and investigated the correlation between relative testis size, a proxy for promiscuity, and the incidence of cooperative breeding, increasing the sample size by an order of magnitude and reducing the northern hemisphere bias of earlier studies. Overall, we found a negative correlation between cooperative breeding and relative testis size, supporting the hypothesis between indirect fitness and cooperative breeding.

INTRODUCTION

Mating systems in animals have a profound impact on virtually every aspect of their lives. Monogamy or promiscuity can affect morphology, spacing, physiology, life history and behavioral traits (Gross and Charnov 1980; Sue Carter et al. 1995; Liu et al. 2001; Preston et al. 2003; Fisher et al. 2013). Understanding the effects of different mating systems has an important role in biology in making sense of apparently maladaptive structures or behaviors (Møller 1988; Zuk et al. 1990a,b, 1992; Sue Carter et al. 1995; Stockley et al. 1997; Lüpold et al. 2009; Fisher and Hoekstra 2010; Stürup et al. 2014). More recently, the revelations of promiscuity in species hitherto categorized as strongly monogamous have necessitated a distinction between social and genetic monogamy (Mulder et al. 1994; Hill and Hurtado 2009). There are major impacts of breeding system effects, including influencing the rates diversification and extinction among lineages (Mitra et al. 1996; Wagner et al. 2012).

The consequences of extra-pair fertilizations (EPFs) in socially monogamous species have profound implications for how we understand the behavior of these animals. Of course, the revelations of social monogamy but genetic promiscuity radically altered how avian mating systems are viewed. Promiscuity introduces uncertainty for both parties in the pair: females with promiscuous males may receive lowered parental care from the male up to complete abandonment of the nest (Neff and Gross 2001; Neff 2003), while males may mistakenly invest heavily in feeding and defense of offspring not their own.

Another major effect of infidelity is how it could affect the evolution of sociality beyond the pair unit. In many social systems, such as cooperative breeding, offspring of a breeding pair do not disperse, and instead remain with the group, to help defend territory and raise siblings as helpers or subordinates (Skutch 1935, Solomon and French 1997; Restrepo and Mondragón 1998, Koenig and Dickinson 2004). In this system, retained adult offspring may benefit from helping raise siblings by providing them fitness in the form of indirect benefits (Hamilton 1964). However, because helpers' indirect fitness is limited by the genetic material they share with these new offspring, non-breeding individuals should be sensitive to the degree of relatedness with the new offspring they are helping to raise. Socially monogamous males may offset fitness losses from cuckoldry by exploiting opportunities to sire their own EPF offspring with neighboring females (e.g. Gibbs et al. 1990). Helpers, however, have no such opportunities for EPFs, and as such must accept any inclusive fitness losses stemming from cuckoldry of their mother. Since helpers are potentially able to breed independently, they should more flexible in their decisions to stay and help, to stay and withdraw helping, or to disperse, and should be more willing to discontinue helping if the breeding female or females are suspected or known by helpers to be promiscuous (but see Welbergen and Quader 2006). If breeding females derive fitness or survival benefits from helpers, the benefits of promiscuity could be outweighed by the costs of losing helpers. This could in turn mean that cooperative breeding would push individuals toward genetic monogamy, or alternatively only arise within genetically monogamous lineages.

Cornwallis et al. (2010) found support for the hypothesis that cooperative breeding is correlated with monogamy using direct measures of paternity in birds. The

authors used published records of clutch relatedness to the breeding male to estimate the correlation between promiscuity and cooperative breeding in a phylogenetic framework, and found a significant negative correlation between promiscuity and cooperative breeding. However, this finding is limited in three important ways: first, while the sample size (267 species) was large enough to detect an effect, this is a small fraction of the roughly ten thousand estimated species of birds (Jetz et al. 2012), and it is possible that this sample is biased. In particular, data on promiscuity were mined from studies that used direct genetic measures of promiscuity. This choice prioritizes what is arguably the gold standard in mating system data over taxonomic breadth. However, these data are biased towards species that are: (a) well-studied and known (e.g. temperate species), (b) are easy to access, or (c) are already suspected to be unusual in their social system or degree of promiscuity. As such, they do not represent a random sample of avian mating systems. Finally, in controlling for phylogeny for all birds, the authors were not able to take advantage of the more recent species level phylogenies (e.g. Jetz et al, 2012), which may provide significant insight into the influence of history on the evolution of both promiscuity and of cooperative breeding. Here we have focused on analyzing a proxy for promiscuity, relative testis size, in order to expand taxonomic and spatial coverage of species and reduce potential bias arising from direct measures of EPFs. This proxy leads to a much larger (an order of magnitude) and less biased sample across all birds.

Relative testis size is a good proxy for promiscuity for two non-mutually exclusive drivers: overall sperm production and sperm competition. Sperm competition is expected to be an important selective factor in promiscuous systems: if males cannot prevent females from copulating with other males, they will attempt to compete with

other males within the female's reproductive tract. The effects of sperm competition leave signatures on male reproductive organs, most importantly the enlargement of the testes (Møller 1988; Moller 1989, 1991; Harcourt et al. 1995; Stockley et al. 1997). First, males mating with multiple females are required to produce more ejaculate than monogamous individuals in the same unit of time. This increase in the need for additional sperm, especially in the case of short, synchronous breeding seasons, where the possibilities for extra-pair copulations are compressed, could select for larger testes in order to meet the demands of increasing copulation rate. Additionally, if females are mating with multiple males, post-copulatory sperm competition may be more important in achieving reproductive success than precopulatory strategies. Indeed, sperm number per ejaculate is associated with promiscuity in mammals and birds (Moller 1989; Pizzari et al. 2003; Laskemoen et al. 2010). In addition, morphological specializations of *spermatozoa* associated with sperm competition (e.g. longer sperm in birds, Briskie and Montgomerie 1992; mammals, Gomendio and Roldan 1991; insects, Stürup et al. 2014; or cooperative sperm morphologies, Fisher and Hoekstra 2010) could require larger testes to produce these specialized morphologies (e.g. large lumen of seminiferous tubules in the case of longer sperm, (Lüpold et al. 2009)) Thus, a strong correlation between promiscuity and high investment in sperm production subsequently selecting for an enlargement of testis mass relative to body mass has been hypothesized and subsequent testing has garnered support from a broad range of taxa (Møller 1988, 1989, 1991; Stockley et al. 1997). If monogamy favors the evolution of cooperative breeding by increasing the indirect benefits of helping, we expect a negative correlation of relative

testis size and cooperative breeding. In this study, we compile data on cooperative breeding and relative testis size across birds to test for this correlation.

METHODS

Testis size measurements were acquired from two sources. First, we used estimates published in Calhim and Birkhead (2007). We supplemented these species with testis length and width measures (in mm) as well as body mass from museum specimens from: The Bell Museum of Natural History, Minnesota; The Field Museum of Natural History, Chicago; Louisiana State University Museum of Natural history; The University of Michigan Museum of Zoology, and the United States National Museum. Bird testes enlarge considerably during breeding season, and reduce in size after breeding (Menaker and Keatts 1968; Stutchbury and Morton 2001). To control for the seasonal nature of testis size, we used testis sizes from specimens that had corroborating evidence of nesting or mating whenever possible (e.g. plumage characteristics, brood patches, observations singing, copulating or tending to the nest), and focused on after first year males, when identifiable by plumage or other characters. In addition, we omitted records that were obviously not in breeding condition (e.g. winter plumage, testis size < 0.1mm, juvenile plumage). We converted long and short axis measurements to mass using Moller's (1991) method. When only one testis size was given, we made the conservative assumption it was the larger of the two testes, as often indicated on specimen tags. To account for an average 8% disparity in size between testes (Calhim and Montgomerie 2015), we multiplied the single testis mass by 1.92. Calculated combined testis mass and

total mass were averaged across individuals for each species. While other authors (Calhim and Birkhead 2007) have advised using polynomial fitting to find the maximum testis size from multiple samples, many species—especially those of tropical origin—were sparsely sampled, which makes fitting a maximum polynomial questionable and potentially misleading (see below for a more complete discussion). Our approach necessarily is conservative regarding the maximum testis size, but should be unbiased with regard to the hypothesis under consideration.

Species in the dataset were then coded as cooperative (1) or non-cooperative (0), as described by Cockburn (2006). The binary binning of social system into cooperative and non-cooperative glosses over considerable variation in the propensity of species to form cooperative groups among populations, the size of those groups, and the social structure within these groups. However, the dearth of multi-population studies for the majority of cooperative species makes it impossible to take these variations into account (but see Koenig and Stacey (1990)). We were conservative in our estimations and used only known cooperative or non-cooperative designations, omitting any species designated as cooperative by taxonomic inference. This sampling strategy for testis size and social system resulted in a dataset of 2,834 species of birds, comprising approximately one third of all named species, and an order of magnitude more species than previous studies investigating the correlation between cooperative breeding and promiscuity. Our data set included 321 cooperative breeders, approximately 11% of the sample (slightly higher than the global 9% of species indicated by Cockburn (2006)). The total number of species included in our study exceeds the minimum sample size (2182 species) suggested for

detecting measures of promiscuity by Calhim and Birkhead (2007) for effect sizes found in previous studies (Moller and Briskie 1995).

We standardized relative testis mass to a variance of 1 and a median of zero. We selected the median as our zero point to reduce sensitivity to the distribution of relative testis size, which skewed away from zero due to outliers. Standardization using these methods appears to be robust, as preliminary analyses using arcsin-transformed data yielded an overall pattern of results nearly identical to median standardized proportions. Sample size for testis varied widely among species (mean sample size: 11.31, range: 1-677). Before our main analyses, we tested to rule out the possibility that sample size of testis measures is a confounding factor. We employed a general linear model (GLM) to test for a correlation between sample size and testis size, and found that while there was a significant positive correlation between sample size and testis size ($\beta=0.0036 \pm 0.00071$, $p=3.24 \cdot 10^{-7}$), the correlation provides little explanatory value (adjusted R^2 : 0.008827). We further tested for a correlation between sample size of testis and cooperative breeding using GLMs, and did not recover a significant effect ($p=0.81$). We concluded that sample size for testes does not produce a major bias in the correlation between testis size and cooperative breeding.

To understand the effects of evolutionary history on the relationship between cooperative breeding and testis size, we used a distribution of stage II trees from Jetz, et al. (2012). These trees comprise a phylogeny of all birds, integrating backbone trees inferred from sequence data with random grafting of unsampled species based on taxonomic information. While these trees have generated some controversy in their applicability (Ricklefs and Pagel 2012), they are the most comprehensive currently

available and should not bias most comparative analyses. The Jetz et al. trees consist of two ‘backbones’ of higher-level relationships inferred by Hackett et al. (2008) (“Hackett backbone”) and Ericson et al. (2006) (“Ericson backbone”). For each backbone, we used a sample of 1,000 trees from the posterior distribution. We manipulated trees and associated tip data within R (R Core Team, 2014), using the package *ape* (Paradis et al. 2004).

We tested for a correlation between cooperative breeding and our proxy for promiscuity using several methods. We first used phylogenetic logistic regression (PLogReg) (Ives and Garland 2010) as implemented in the R package *phylolm* (Ho and Ane 2014). We used Tjur’s method of calculating a pseudo- R^2 in order to assess the goodness of fit for logistic regression (Tjur 2009). Briefly, this method calculates the difference between the means of the predicted values of the two binary responses. In addition to logistic regression, we analyzed these data using phylogenetic generalized linear mixed models, as implemented in the R package *MCMCglmmRAM*. We used a flat, uninformative prior, and due to the high degree of phylogenetic heritability in our phylogeny, used a reduced threshold model and set the phylogenetic heritability to 1 (Hadfield, pers. comm.; Hadfield 2015).

To compare our results based on testis size to those from direct measures of promiscuity, we used the data compiled by Cornwallis et al (2010), matched to species with testis size information, for a total of 181 species. To directly compare with our testis data, we median-standardized the fraction of nests with the presence of extra-pair nestlings to account for the skew towards zero, and regressed these data against cooperative breeding with phylogenetic logistic regression as above, with a subset of 100

randomly selected trees with the Ericson backbone. For comparison, we performed the same regression using testis data for the same subset of 181 species.

RESULTS

Phylogenetic logistic regression

For both the Hackett and Ericson backbones, we found all trees produced significant results (average p-value Hackett Backbone: $1.52 \cdot 10^{-78} \pm 1.37 \cdot 10^{-78}$, Ericson Backbone: $1.34 \cdot 10^{-81} \pm 1.06 \cdot 10^{-81}$, Table 2.1). For both backbones, testis size was found to show a negative correlation with cooperative breeding (Hackett mean = -0.55 ± 0.02 ; Ericson mean = $-0.55 \pm .02$, Table 2.1). Our model found a Tjur's R^2 of 0.142, suggesting that testis size provides moderate explanatory value for these data (Figure 2.1). The phylogenetic correlation parameter (alpha) showed a weak phylogenetic correlation (Hackett: mean $\alpha = 0.012 \pm 2.0 \cdot 10^{-05}$; Ericson: $\alpha = .012 \pm 2.15 \cdot 10^{-05}$, Table 2.1), consistent with a model of Brownian motion for a continuous trait (Ives and Garland 2010) and suggesting testis size is not highly influenced by phylogenetic history.

MCMCglmm regression

MCMC analyses were run for 70,000 iterations, discarding the first 10,000 iterations as a burn-in, with a sampling interval of 150 iterations. All trees produced an effective sample size >300 . In contrast to the logistic regression results, the MCMCglmm regressions were not significant for the nearly all trees sampled in both the Hackett and Ericson backbones (Hackett: 1.7% significant, Ericson: 1.5% significant). In addition, the

coefficients for all trees were generally positive (Ericson: 96.9% positive slope, Hackett: 97.7% positive slope, Table 2.2). Average coefficients were positive but generally overlapped with zero (Table 2.2), suggesting no relationship between cooperative breeding and testis size using MCMCglmm methods.

Direct measures of promiscuity

We validated our proxy using direct measures of paternity. This analysis used a substantially smaller dataset than our main analyses (approximately 6% of the total records). However, we found that direct measures of extra-pair fertilizations were significant ($p < 0.05$) in 97 of the 100 trees tested. In addition, the slope of the response was uniformly negative (mean $\beta = -0.415 \pm 0.111$) (Table 2.3). The magnitude of this slope is less negative than the full testis size dataset, but is similar in magnitude. Repeating this analysis using relative testis size for the same species produced 29 of 100 significant trees. However, the slope of the response for all trees was negative, even if non-significant (mean $\beta = -0.183 \pm 0.0656$, Table 2.3). Assuming that a relationship between monogamy and cooperative breeding truly exists, this suggests that our proxy is an unbiased but less precise measure of promiscuity.

DISCUSSION

We investigated the hypothesis that relative testis size—a proxy for promiscuity—is negatively correlated with cooperative breeding. This finding would

support the theory that helpers are sensitive to indirect benefits, which are modulated by relatedness to new young in the group.

Phylogenetic breadth and use of testis size as a proxy for promiscuity

Use of testis data rather than genetic measures of promiscuity substantially increased the sample size and phylogenetic breadth for testing the effects of promiscuity. Our study adds six orders and at least 51 families to the comparative analysis of promiscuity and cooperative breeding (Appendix Figure 2.2), along with numerous additional species for clades previously included, increasing sample size by an order of magnitude (266 species in Cornwallis, 2010 compared to 2843 species in this study). The addition of multiple suboscine passerine families increases the sampling of the Neotropics, the peak of suboscine diversity and a major component of species diversity in the Neotropics. Likewise, the addition of Columbiformes, Caprimulgiformes and Trogoniformes adds rarely sampled diversity to the dataset and improves the representation of promiscuity in non-cooperative birds. Of particular note was the addition of multiple families, especially Lybiidae, Ramphastidae, Semnornithidae, and Galbulidae, including critical cooperatively breeding lineages in the order Piciformes.

In addition, we substantially increased the biogeographic coverage of the study, especially in the tropics. This increase is apparent both in raw numbers of species and the percentage of the sample that occur in the tropics as compared to the Cornwallis dataset (Figure 2.2). The largest proportion of the Cornwallis dataset was from the Palearctic and Nearctic, while the most coverage of any tropical region was from Australia. This pattern suggests a significant temperate species bias in this dataset. Use of relative testis size

allowed us to increase sample size overall, and to especially increase the proportion of species residing in the tropics, especially in the Neotropics and Africa. This expansion provides a regional distribution more reflective of the global distribution in birds and reduces geographic bias towards temperate species in particular.

Phylogenetic logistic regression reveals a negative correlation between cooperative breeding and promiscuity

Our results from phylogenetic logistic regression (PLogReg) demonstrate a significant, negative relationship between cooperative breeding and promiscuity. These results were robust to the phylogeny, and were significant for both trees selected from the posterior distribution of species-level trees and for trees with different high-level topologies. Our findings support and extend those of Cornwallis, et al (2010), and suggest that cooperation is associated with both lower promiscuity and smaller testis size, as suggested by kin selection theory. Our findings also suggest that the inclusion of a greater diversity of non-cooperative species and the use of testis size as a proxy for promiscuity does not change the estimated impact of promiscuity on the origin of cooperative breeding. Tjur's R^2 indicated a moderate fit, suggesting that some of the variance is explained by promiscuity. It is unclear if this percentage is underestimated due to variation associated with our measurements of testis size (see below) or if there are other factors that are required to drive the evolution of cooperative breeding (as suggested by Cornwallis et al. (2010)). Our results are similar in magnitude to those of Cornwallis, suggesting that issues associated with estimating promiscuity using relative testis size are not significant enough to negatively impact our study.

MCMCglmm versus PLogReg methods for comparative studies

We found discordant results between PLogReg and MCMCglmm methods. While PLogReg results were uniformly significant and predicted a negative association between cooperative breeding and testis size across all trees, MCMCglmm had almost no significant results across the distribution of trees (Table 2.2). In addition, the correlation between cooperative breeding and testis size was almost entirely (97.7% Hackett, 96.9% Ericson) positive across the trees. This suggests that the correlation between cooperative breeding and testis size is sensitive to the method of analysis.

However, the disjoint results between the PLogReg and the MCMCglmm results do not invalidate our findings due to important differences in how the methods differ in their treatment of binary response variables and how they estimate their predictors. PLogReg explicitly models the evolution of a binary trait along a phylogenetic tree, while MCMCglmm uses a covariance matrix to remove the effect of phylogenetic history, rather than treating it as an explicit process. The power for PLogReg is increased compared with MCMCglmm methods due to explicitly modeling the evolution of a binary trait down the tree (Ives and Garland 2010). Interestingly, in simulation tests of PLogReg demonstrate a lower incidence of type I errors than other methods. If PLogReg is a better indicator, it would suggest that it would be *less* likely to demonstrate false positives. This study, however, used predictors that were *positively* correlated with the response, rather than negatively correlated. We interpret the pattern of nonsignificant results and positive predictors from our MCMCglmm analysis as a symptom of upward biases for the predictor under standard logistic regression (Ives and Garland 2010). If the

true correlation between the testis size and cooperative breeding is negative, an upward bias would move the predictor closer to zero and thus eliminate a significant signal. This could in turn produce the false negatives we observe, and explain why we observe false negatives rather than false positives in our MCMCglmm regression as compared to our PLogReg.

Comparison with direct measures of promiscuity

The slopes found for both backbones are slightly more negative than, but still consistent with results found by Cornwallis et al. (2010) ($\beta=-0.27$). There are two potential explanations for this finding. First, the expansion of sampling may have increased the number of highly promiscuous species included in the sample, which is reflected in the tail of very large relative testis sizes. Second, due to difference in testis size and methods of measuring them, the testis data may be a less accurate representation of the true mean than direct, genetic sampling of offspring.

Direct, genetically-determined measures of extra-pair paternity have been critical in advancing our understanding of promiscuity. The drawbacks of using these methods are mostly those of cost and access to sufficient nests to gain a sufficient sample size to determine population- or species-level rates of extra-pair offspring. Our results using direct measures of extra-pair copulations demonstrate several important caveats to the use of relative testis size as a proxy for promiscuity. First, our application of the logistic regression approach replicates the response reported by other methods (MCMglmm; Cornwallis et al. 2010), suggesting that these findings are robust to methodology. Our findings for direct promiscuity were slightly less strong than those reported by

MCMCglmm (mean $\beta = -0.63$, CI = -0.86 to -0.33 for MCMglmm versus mean $\beta = -0.41 \pm 0.11$ for PLogReg, Table 2.3), but largely within the confidence interval. This difference is likely due to a 32% reduction in sample size due to non-overlap between the direct measures of promiscuity and testis size datasets (181 species vs. 266 species). Importantly however, the correlation between relative testis size and cooperative breeding was much less consistent across phylogenetic hypotheses for the same number of species (29% significance of relative testis size versus 97% significance of direct measures of EPF, Table 2.3). We interpret this as significantly more variation in relative testis size than EPF rates, most likely driven by variation in seasonal testis size, discussed below.

However, when comparing direct measures of promiscuity to the larger dataset of over 2,800 species, we find considerable accord between relative testis size and direct measures of paternity. When using relative testis size, larger datasets appear to provide sufficient statistical power to estimate rates of promiscuity, even with the limitations of this data type outlined below. Our ability to use relative testis size as a proxy for promiscuity opens the door to larger, multi-factor correlational studies of the determinants of cooperative breeding.

Testis size determination and considerations for temperate versus tropical species

While active growth and maintenance of museum collections has declined in many institutions for the last several decades (Suarez and Tsutsui 2004), they provide critical scientific data, not only as a repository for type specimens or other historical records, but as a source of data for a wide range of ecological and evolutionary topics

(Moksnes and Røskoft 1995; Shaffer et al. 1998; Cheng et al. 2011; Snell-Rood and Wick 2013). Our use of museum collections to investigate the effects of mating system on social behavior, as well as previous comparative studies of testis size, reiterates the usefulness of collections-based data. Current progress in direct estimation of EPF rates among bird species is fairly limited compared to the volume of data accessible in museum collections, and while EPF data may be much more accurate for individual species, excessive dependence on this gold standard can also lead to biased sampling (Figure 2.2). Finally, while all scientific work in birds generally has biases towards northern hemisphere and temperate species similar to EPF data, collections often house specimens of rare and unusual species, and generally have more complete tropical sampling than is currently available in direct measures of EPFs. If records are both meticulous and complete, these specimens can help us improve our understanding of these species in a global comparative context. One challenge in using collections-based data is the lack of uniform data standards. The online compendiums of avian museum records, (e.g. *Ornis*, VertNet; Constable et al. 2010; www.vertnet.org), while helping to provide information on where particular species are located, and species and collection date information, provides gonadal measurement data in a notes section, if at all. Notes sections, due to differences in transcription, do not allow efficient automated extraction of information. While some institutions provide full biometric information online, post-processing extraction is still often necessary. An accessible database standard with explicit incorporation of morphometric data would be helpful in alleviating these issues.

Caveats

While we found a strong negative correlation between cooperative breeding and promiscuity, there are several caveats to the interpretation of these results. First, cooperative breeding occurs in a range of social systems. Perhaps the most commonly recognized cooperative breeding system is that of a breeding pair and its retained offspring. By contrast, cooperative systems also includes other systems such as those where multiple breeding pairs and helpers defend a common territory (e.g. African Starlings, (Rubenstein 2007)), or where multiple, (largely) genetically-monogamous pairs lay eggs into a single nest and defend and provision young without regard to parentage (Riehl 2012). These differing social structures should have different relationships with promiscuity than the canonical single-family social structure that is predicted to place a premium on monogamy. For instance, while promiscuity is low, female starlings in multiple-pair groups pursue extra-pair mating strategically to either increase the number of helpers or to increase their offspring's heterozygosity depending on their circumstances (Rubenstein 2007). Currently, documentation of the social structure in cooperative breeders is haphazard, but inclusion of this information is important to understanding if there is a single selective force or set of forces shaping the evolution of cooperative breeding, or if these behaviors are a common solution to a wide range variety of lineage-specific drivers.

Second, our information on testis size is limited by our understanding of breeding systems in tropical birds, which may lead to an underestimation of relative testis size. Breeding in temperate areas is driven by seasonal changes intimately connected with predictably changing photoperiod, making the onset of breeding and subsequent testis

enlargement relatively straightforward and synchronized (e.g. Menaker and Keatts 1968). The tropics, by contrast, are often driven by smaller scale changes in climatic patterns, including the onset or end of rainy seasons, which may occur several times annually. These rainy seasons can be driven by predictable annual cycles (e.g. monsoon seasons), but can also be driven by cycles with multi-year durations (e.g. el Niño Southern Oscillation) (Stutchbury and Morton 2001). In addition, unlike photoperiod-derived seasonality, tropical rainfall onsets can be heavily influenced by regional and local conditions and topography. All these factors make it more difficult to broadly predict the onset of breeding seasons across species in the tropics. Compounding this uncertainty around breeding season, tropical species are also more sparsely sampled. Major collecting expeditions occur more infrequently and are often more constrained by funding and time to collect compared with temperate collecting expeditions. Subsequently, areas are sampled relatively infrequently and incompletely. Combined with less predictable (and potentially less synchronized) breeding seasons, it is more likely that we are not sampling effectively during the breeding season, and subsequently underestimate relative testis size in tropical birds. This is especially pertinent when investigating cooperative breeding, because the majority of cooperative breeders are found in the tropics (Stacey and Koenig 1990, Arnold and Owens 1999; Stutchbury and Morton 2001), meaning our results could be biased toward smaller testis size. While recognizing these limitations, we feel that our extension of the geographic and species coverage, reduction in bias towards temperate species, partial cross validation using direct measures of promiscuity, and the increased power afforded by using relative testis size justifies the interpretation of our findings and the use of relative testis size as a proxy for promiscuity.

CONCLUSION

We found a well-supported negative correlation between cooperative breeding and relative testis size in birds in phylogenetic logistic regression, which we argue is due to testis size reflecting genetic promiscuity in birds. Our results thus corroborate and extend a previous study finding a correlation between cooperative breeding and direct measures of promiscuity (Cornwallis, 2010). Furthermore, we found that while testis size required a greater sample size to achieve significance, the correlation between cooperative breeding and testis size was similar in magnitude to those found for cooperative breeding and direct measures of paternity. Our use of testis size expands the sampling of all birds, especially of non-passerine and tropical species, and produces a sample less biased towards temperate, northern hemisphere regions than previous attempts. Our approach adds credibility to the judicious mining of museum collections for non-traditional morphological datasets, and we suggest improvements in the accessibility and dissemination of these data. Improvements of current data will require a better understanding of breeding seasonality in the tropics, both at the species level (e.g. species-level response to environmental cues), and a better understanding of tropical seasonal conditions (e.g. regional differences in the onset and end of rainy seasons). These improvements will increase the accuracy of our estimates of maximum testis size. In addition, these findings also highlight a need for continued focus on tropical research and collecting expeditions. While we have vastly improved the sample size of birds in the tropics, many are represented by a handful of specimens or even a single individual.

Improving the sample size per species as well as finding better estimators of breeding times, especially for the tropics, will be important for increasing the reliability of these data. While the correlation reported here is significant, it only provides a partial explanation for why cooperative breeding has evolved (Cornwallis, 2010): many species are monogamous, but relatively few are cooperative. The application of models that can take into account the contributions of both promiscuity (via testis size as a proxy) and other possible drivers such as climate, predation rates, and brood parasitism (Jetz and Rubenstein 2011; Feeney et al. 2013) will allow estimation of the relative importance of these factors in the evolution of cooperative breeding for a substantial fraction of avian diversity.

Table 2.1— Parameter estimates for Phylogenetic Logistic Regression (PLogReg).

Tree Backbone noted as “Hackett” or “Ericson”. All parameters are averaged across the sample of 1000 trees. α indicates the strength of the phylogenetic signal, with an $\alpha=0$ equivalent to a continuous trait evolving under Brownian motion. β indicates the estimate of the correlation between cooperative breeding and relative testis size.

Parameter	Mean	SE	p
Hackett β	-0.55	± 0.02	1.52 E-78
Ericson β	-0.55	± 0.02	1.34 E-81
Hackett α	0.013	± 2.0 E-5	--
Ericson α	0.012	± 2.0 E-6	--

Table 2.2— Parameter estimates for MCMC generalized mixed models

(MCMCglimm). Tree Backbone noted as “Hackett” or “Ericson”. All parameters are averaged across the sample of 1000 trees. β indicates the estimate of the correlation between cooperative breeding and relative testis size.

Parameter	Mean	Mean Lower 95% CI	Mean Upper 95% CI	p
Ericson β	0.013	-0.015	0.041	0.39
Hackett β	0.013	-0.015	0.042	0.38

Table 2.3— Comparison of parameter estimates of Phylogenetic Logistic Regression (PLogReg) of direct (genetic) measures of promiscuity versus indirect (relative testis size) measures of promiscuity. All parameters are averaged across a sample of 100 trees. α indicates the strength of the phylogenetic signal, with an $\alpha=0$ equivalent to a continuous trait evolving under Brownian motion. β indicates the estimate of the correlation between cooperative breeding and relative testis size.

Parameter	Mean	SE	p
EPF β	-0.41	± 0.11	0.0034
Testes β	-0.183	± 0.07	0.26
EPF α	0.011	--	--
Testes α	0.011	--	--

Figure 2.1— Relative testis size data plotted against cooperative (1) and non-cooperative (0) species and fitted to a logistic curve. Note the weak, but distinctly negative slope of the curve.

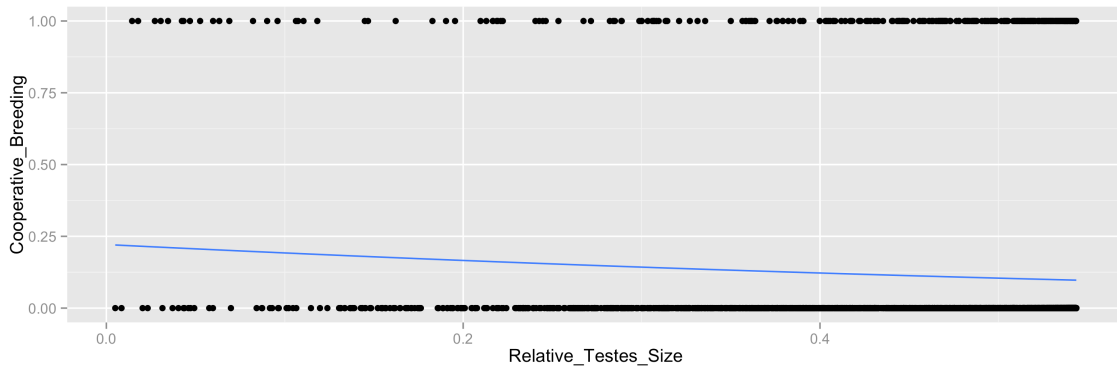
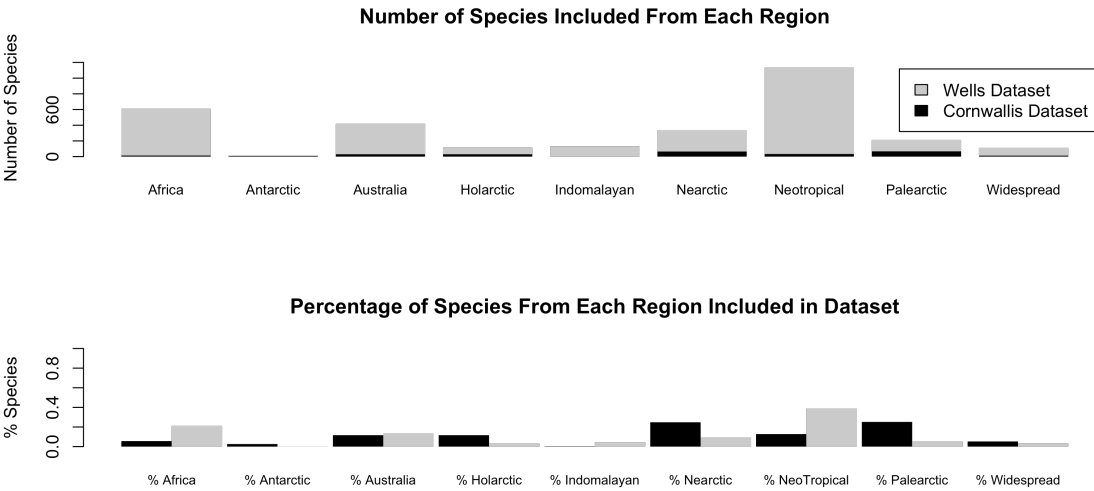


Figure 2.2— Regional differences in data coverage for Cornwallis and this studies’

data. (a) Number of species in each region in datasets of Cornwallis, 2010 and this study’s data. Note the great expansion of the number of species included in the data for all regions. (b) Proportion of total dataset from each region for Cornwallis, 2010 and this study. Note the high bias towards temperate species (Nearctic, Palearctic) in the Cornwallis dataset, and the relative lack of species from the highly speciose African and Neotropical biogeographic regions.



CHAPTER 3

AN INTEGRATED MULTIFACTOR COMPARATIVE ANALYSIS OF COOPERATIVE BREEDING IN BIRDS

Global scale comparative analyses have implicated a number of hypothesized drivers of the evolution of cooperative breeding, including monogamy, precipitation uncertainty, and brood parasitism. However, each of these hypotheses has been tested independently, and it is unclear which, if any, of these drivers have the greatest causative effect on the evolution of cooperative breeding globally. In addition, no studies have looked at the potential interactions between these hypothesized drivers and how combinations may drive cooperative breeding. Using both Bayesian and Maximum likelihood analyses, we investigated the relative importance and interactions of five hypothesized drivers of cooperative breeding in birds, at both regional and global scales. Brood parasitism was the most consistent driver across analyses, while other traits had varying support, depending on the choice of analysis and phylogenetic tree, and interactions were poorly supported. Overall, we found that choice of analysis and phylogenetic tree had profound effects on the outcomes of our analysis, suggesting additional work needs to be done both in collection of trait and phylogenetic information, as well as investigations into comparative analysis methods.

INTRODUCTION

Social living in animals is considered one of the last major organizational innovations of living organisms (Maynard Smith 1995). How species evolve sociality, especially when the interests of the individuals comprising the group may not be always be aligned, has major implications for speciation, demographics, and life history (Cockburn 2003) for a variety of species, including those of humans (Hrdy 2007). Understanding how group living evolved has generated considerable interest among biologists (Stacey and Koenig 1990; Clutton-Brock 2002, 2009; Ligon and Burt 2004; Nowak et al. 2010). While this interest has traditionally manifested itself in the study of highly complex eusocial animal societies (Hamilton 1964; Wilson and Hölldobler 2005; Nowak et al. 2010), this may not be the best approach to understanding how sociality evolves. Most eusocial species contain group members that are unable to reproduce independently, and subsequent evolution after the loss of independent reproduction likely obscures the origins of group living. A potentially more fruitful approach to understanding the factors involved in evolving group living is through study of social systems with multiple, more recent shifts to sociality. One such system is cooperative breeding, where three or more adults help raise offspring together (Skutch 1935; Brown 1987; Stacey and Koenig 1990; Koenig and Dickinson 2004). In addition to the individuals reproducing ('breeder' or 'dominants'), this system includes non-reproducing individuals ('helpers' or 'subordinates') that are capable of breeding and living independently (Brown 1987), but do not. This relatively simple social structure, as well as comparative analyses of its distribution among species, suggest that the origins of

group living are more recent, and therefore its drivers are less likely to be obscured by subsequent evolutionary and environmental change. To date, hypotheses for the origins of cooperative breeding emphasize three major effects: genetic relatedness and its impact on kin selection (Hamilton 1964; Cornwallis et al. 2010), the impact of broad climatic challenges on independent breeding (Arnold and Owens 1999; Jetz and Rubenstein 2011), and the impact of particular biotic drivers (Poiani and Elgar 1994; Clutton-Brock et al. 1999; Feeney et al. 2013).

Genetic relatedness between group members provided the first viable explanation for the formation of cooperative groups. Foremost is Hamilton's inequality (Hamilton 1964), which posits that genetic fitness can be accrued by increasing the fitness of related individuals (indirect benefits or indirect fitness). Hamilton's inequality, while formulated to better understand the evolution of eusociality (Hamilton 1964), has been applied with success to the phenomenon of cooperative breeding. Indeed, recent work by Cornwallis et al. (2010), investigating the relationship between the proportion of extra-pair copulations in female birds and the likelihood of cooperative breeding, found a general negative correlation between promiscuity and cooperative breeding, as well as evidence for better kin recognition in cooperative breeders with higher promiscuity (Chapter 2). Taken together, these results suggest that cooperative breeding is associated with breeder mate fidelity. However, this finding is predicated on a particular social structure; specifically, that helpers are either retained offspring or close relatives of one or both of the breeding pair (e.g. siblings). A nuclear-family social structure may act to limit promiscuity because females lack easy access to alternate mates due to incest avoidance in the group. While the nuclear family social system is common, species with co-nesting pairs (e.g. groove-

billed anis, (Vehrencamp 1978)), complex clan based social structures (e.g. crows and starlings (Wilkinson 1982; Stacey and Koenig 1990)) and kin neighborhoods (e.g. long-tailed tits, (Hatchwell 2009)) are all also considered cooperative breeders, and are coded as such. These social structures, due to the greater access of potential mates, may have evolved cooperation in ways that do not follow a kin-selection paradigm. Also, while low promiscuity may set the stage for cooperative breeding and could act to maintain cooperative groups, it does not provide an explanation for what actually drives the evolution of group formation in some but not all genetically monogamous species; in addition, it is unclear if monogamy is a minor or major contributor to the evolution of cooperative lineages. Finally, it is possible that genetic monogamy is actually a byproduct of sociality, through retained offspring increasing their own fitness by enforcing monogamy on their mother (Welbergen and Quader 2006).

The importance of ecological factors also has a long history in the study of cooperative breeding. One early theory—the so-called habitat limitation hypothesis—was that the lack of suitable territories for new recruits to the population (Emlen 1982) led to offspring retention and cooperation. Under this theory, we would expect that cooperative breeders are species constrained by habitat preferences in areas of high habitat heterogeneity. The lack of suitable territories would lead to extended residence and cooperation, the latter as a byproduct of the lack of dispersal.

However, habitat limitation is a proximate mechanism, and fails to explain broad geographic patterns of sociality, such as an apparent latitudinal bias of the distribution of cooperative breeding towards tropical environments. Instead, other broad-scale ecological drivers of cooperation may have better explanatory value. Two competing

options that would better explain the latitudinal trends in cooperation have been put forward: seasonality and environmental unpredictability.

In an *aseasonal* environment, large shifts in resource availability and environmental harshness are minimized. This would potentially minimize offspring mortality and allow young to accumulate in and around the parents' territory, increasing population density and local saturation. This situation could set up either a retained-offspring scenario due to habitat saturation or extended post-fledging period, which in combination with kin-selected behaviors drives the evolution of cooperative breeding. Alternatively, if dispersal distances are small, this could drive the formation of a kin neighborhood (Arnold and Owens 1999; Hatchwell 2009). This scenario would explain the general trend towards more cooperative species in tropical habitats, but does not provide a clear explanation for the occurrence of cooperation in arid or temperate zones.

Recent work has suggested that cooperative breeding may be driven by environmental *uncertainty* especially uncertainty in resource availability and climatic extremes, and their effects on subsequent likelihood of survival in dispersing young. Uncertain environments could set up a bet-hedging scenario where offspring stay with their parents, gaining access to resources during bad times and accruing indirect fitness by raising siblings, and during good times either dispersing to breed independently or accruing high levels of fitness by helping already established group-mates produce large numbers of highly related offspring. Jetz and Rubenstein (2011) found evidence for cooperative breeding occurring more frequently in areas with high levels of interannual variance in precipitation and temperature. However, this does not explain cooperative breeders found in stable environments such as rainforests (e.g. Gonzalez et al. 2013).

Finally, biotic interactions have been proposed to favor the formation and maintenance of social groups. Work on fairy wrens has found that larger groups are more effective at repelling brood parasites, subsequently increasing the fitness of groups and individuals (Feeney et al. 2013). It has been proposed that the evolution of cooperative breeding may even be driven by these factors (Feeney et al. 2013), although other work (Chapter 1) suggests that this association between parasitism and cooperative breeding may be a byproduct rather than a driver of cooperative breeding. Predation is also a possible driver for cooperative breeding, as larger groups are more effective at both detecting and driving away predators through mobbing actions (Clutton-Brock et al. 1999; Graw and Manser 2007).

All of these proposed drivers have found some support in individual comparative analyses (Arnold and Owens 1999; Cornwallis et al. 2010; Jetz and Rubenstein 2011; Feeney et al. 2013). However, to date, all of these hypotheses have been tested in isolation. It is currently unclear what the relative importance of each factor might be in the evolution of cooperative breeding. In addition, it is likely that combinations of factors may need to be present or could be interacting with one another in ways that drive the evolution of cooperatively breeding lineages, better explaining the observed patterns than any single factor. Additionally, it is unclear if ecological factors are consistent across cooperatively breeding lineages, or if ecological drivers are idiosyncratic to each lineage. In this study we take an approach that combines these relevant factors into a single analysis to determine their relative importance and possible interactions. Specifically, we analyze the occurrence of cooperative breeding in birds in the light of multiple predictive factors, employing a model selection approach to determine the best model with no a

priori assumptions regarding the relative importance of factors or combinations of factors. Given our current understanding of the evolution of cooperative breeding, we might expect to find an interaction between promiscuity and one or more ecological factors sparking the transition to cooperative breeding, but the specific drivers may vary by region. Scale is highly important in ecological factors: while there may be a global pattern for each of these factors, it may be driven by especially strong signal one or a few areas. For instance, the finding that interannual variance is correlated with cooperative breeding is especially strong in Australia and Africa (Jetz and Rubenstein, 2011), and may swamp out other signals from other regions (e.g. the Neotropics). Both global and regional approaches are needed to tease apart the importance of regional ecological drivers. Due to broad differences in the ecological factors across continents, we further analyzed models by biogeographic region to determine if ecological patterns are being hidden by region-specific differences in ecological circumstances.

METHODS

To evaluate the relative importance of possible determinants of cooperative breeding, we built a dataset combining information on social system, records of brood parasitism, relative testis size (a proxy for promiscuity (Chapter 2)), and several environmental measures.

We used Cockburn's (2006) compilation to identify cooperatively-breeding bird species. To maximize sample size we used his inferred list of cooperative breeders as our basis for determining cooperative or non-cooperative species. To date, this is the most

complete compendium of breeding system data in birds. We updated this list with both primary literature changes and the recommendations of Ligon and Burt (2004), and coded cooperative breeding as a binary trait (0 for non-cooperative, 1 for cooperative).

To address the impact of environmental stability, uncertainty, and heterogeneity, we used the ecological dataset of Botero et al. (2014), which provides information on the species range mean precipitation and temperature predictability, as well as measures of environmental harshness and precipitation unpredictability for 6694 bird species. To reduce the number of ecological factors, we subjected our ecological variables to a principal components analysis, standardizing to z-scores and centering the data, as well as standardizing variance when necessary. As predictors, we chose the top three principal components, which explain 81% of the total variance in the data (Table 3.1). Loadings for the first principal component (PC1) are mixed across several parameters with none dominating. However, larger values on this scale are associated with warm, wet, high net primary productivity (NPP) environments with predictable temperature and precipitation. The second principle component (PC2) is dominated by a strong negative loading on precipitation predictability (higher values therefore indicate unpredictable precipitation). Our third principle component (PC3) is dominated by habitat heterogeneity as defined by the number of biomes exceeding 5% of habitat in a species' range (Olson et al. 2001; Botero et al. 2014), and to a lesser extent, predictability of precipitation.

Estimation of extra-pair fertilization rates is difficult, as genetic monogamy rarely corresponds to social monogamy in birds (Davies 1985; Gibbs et al. 1990; Mulder et al. 1994). Due to the limited number of species that have had their mating systems evaluated using genetic data, in this study we use relative testis size as a proxy for extra-pair

paternity, which recovers the same negative correlation of promiscuity with sociality as that found by Cornwallis et al, but for a much larger sample of species (Chapter 2). The methods for testis size estimation are outlined in Wells and Barker (Chapter 2), but are outlined briefly here. Specifically, we used testis size measurements from museum collections and published sources (Calhim and Birkhead (2007), USNM, Field Museum, Bell Museum, UMMZ, LSUMNS) to estimate the relative size of the combined testes in breeding season to body mass for the species, then standardized these measures to a median of zero and a variance of 1.

Finally, we determined if each species hosted brood parasites using the compendium compiled by Lowther (2012). In the case of *Molothrus*-parasitized species, we conservatively coded any species with fewer than 10 records of parasitism as non-parasitized. Similarly, we coded all other hosts that were ‘uncertain’, ‘possible’, or ‘likely’ as unparasitized. Records could be biased in that species coded as ‘non-parasitized’ may in fact be parasitized but parasitism has not observed and recorded. Conversely, some species with reports of parasite eggs in the nest may not be effective hosts, but this is difficult to document. However, our conservative estimates should provide reliable data on the incidence of brood parasitism in birds.

Collation of data from these disparate, imperfectly overlapping sources resulted in a dataset of 2,321 species with no missing values, representing roughly a quarter of all bird species.

To account for the influence of phylogenetic history on variable correlations we used trees derived from Jetz et al. (2012). That study provided a comprehensive, species-level phylogeny for all birds through supertree construction and random grafting of taxa

with missing data based on taxonomic constraints. The resulting trees were produced from two different hypotheses of high-level relationships between clades (“backbones”): 1) the trees inferred by (Ericson et al. 2006), and 2) the trees inferred by (Hackett et al. 2008). These are referred to as the “Hackett” and “Ericson” backbones, respectively, throughout the text. While the Jetz et al. trees have generated significant controversy (Ricklefs and Pagel 2012), the advantages of enlarging the comparative dataset are compelling; however, given known and potential issues with these trees (Barker et al. 2015; Rabosky, in press), interpretation of comparative analyses based on them should be carefully considered. Since the posterior distribution of Jetz trees can vary substantially in details that could affect comparative analyses, we used 100 randomly selected trees from the 10,000 tree posterior distribution in order to address this variation, and summarized results across all trees.

We analyzed this dataset using the phylogenetically corrected Bayesian mixed models, as implemented in the package *MCMCglmm* in R (Hadfield 2010), using a binary response (cooperative or non-cooperative). Phylogeny was included as a random effect in the model (coded using the “animal” pedigree), and fixed effects being the predictors and their interactions (see below). Preliminary analyses suggested that the phylogenetic heritability approaches 1 in this model, which can cause problems with convergence. To rectify this issue, we used a threshold family model as implemented in *MCMCglmmRAM* (Hadfield 2015), with G-variance structure fixed at 1, and R-variance set to $1e-16$. We checked for convergence visually, and extended chains so as to ensure effective sample sizes of >200 for all parameters. Given that each potential correlate of sociality being evaluated here has been found significant independently, we had no clear *a priori*

expectations for how these factors may interact with one another and instead employed a model-selection approach, implemented in R using the *dredge* function of the *MuMIn* package (Barton 2013), using the Akaike information criterion corrected for small sample size (AICc). We evaluated the correlation structure among all of the primary factors (brood parasitism, testis size, and three ecological PCs) by regression, and omitted interactions from any significantly correlated primary factors, resulting in a global model with 13 terms. We assessed the strength of evidence for the top models using ΔAICc , model weights, percentage of trees including the model as a top ($\Delta\text{AICc} \leq 2$) model, and evidence ratios.

Results from phylogenetic models using logistic regression have issues with inflated means (Ives and Garland 2010). In previous work, we found discordant results in the predictors of relative testis size when regressed against cooperative breeding using generalized linear model methods as opposed to phylogenetic logistic regression, most importantly changing the sign of the predictor from positive to negative. Due to this issue we also evaluated the predictors of our top models using the phylogenetic logistic regression as implemented in the R package *phyloglm*, in a maximum likelihood framework, and increasing the linear search space (“btoI”) to 80 (Ho and Ane 2014). Because *phyloglm* is not compatible with *MuMIn*, we ran the same model combinations independently and calculated relevant statistics (ΔAICc , model weights) using the combined outputs of all models. To better understand the relative importance of model parameters across the top models, we used model averaging to estimate the parameter values and parameter weights across the top models ($\Delta\text{AICc} \leq 2$) for both generalized linear model and phylogenetic logistic regression methods.

One possible reason for the significant findings of so many separate predictors of cooperative breeding is that there are different drivers in different regions and each predictor on its own swamps other drivers when considered alone. Since many ecological and life-history traits are not uniformly distributed globally, we broke our dataset into 5 biogeographic regions (Africa, Australia, the Palearctic, the Nearctic, and the Neotropics) and repeated our model-selection procedures from the global runs in a subset of 10 trees from each backbone in order to ascertain if different regions favored differing predictors of cooperative breeding or if the predictors of cooperative breeding were globally consistent. Sample size for these regional data sets ranged from 1039 species (Neotropical) to 118 species (Palearctic). We omitted three categories, ‘widespread’, which consisted of birds living in two or more biogeographic regions as being less informative and ‘Holarctic’ and ‘Indomalayan’ due to low sample size.

RESULTS

Global analyses of cooperative breeding

We ran each generalized linear model function using *dredge* for 90,000 iterations, discarding the first 10,000 iterations as a burn-in, and thinning chains every 150 iterations. Using *dredge*, we compared the fit of 235 combinations of predictors of cooperative breeding (5 main predictors and 8 interactions). For phylogenetic logistic regressions, >99% of the 235 models per tree completed analysis successfully in the original linear search space. Analyses of the remaining models were completed interactively, using different search space parameters until they successfully ran to

completion. We report models using combinations of terms (Host=status as host of a brood parasite, Testis=relative testis size, PC1=environmental variable principle component 1, PC2=environmental variable principle component 2 and PC3=environmental variable principle component 3) separated by “+” signs (e.g. “Host + Testis”) and interactions among terms using “:” between the terms (e.g. interactions between PC1 and PC3 would be reported as “PC1:PC3”).

For the global dataset, the posterior trees analyzed identified several equally likely models in the generalized linear model analysis ($\Delta AICc < 2$, Backbone mean number of models per tree: Hackett, 3.6 ± 2.01 ; Ericson, 3.8 ± 2.59). Overall, we found 29 and 37 models were included as best fits for the 100 randomly selected Hackett and Ericson backbone trees, respectively (Appendix Figure 3.1, Appendix Table 3.2, Appendix Table 3.3). For the global dataset in the phylogenetic logistic regression analysis, there were generally more top models ($\Delta AICc < 2$) per tree than in the generalized linear model runs (Hackett: 6.17 ± 4.03 , Ericson: 5.97 ± 3.71). Overall, phylogenetic logistic regression included 79 and 76 models as best fit for Hackett and Ericson, respectively, nearly double that of the generalized linear models analyses.

Model averaged weights across top models of generalized linear models returned up to 10 and 8 terms in the Ericson and Hackett backbones, respectively. The highest-weighted terms for both backbones were Testis and Host, while ecological factors had much lower weights, indicating lower model support (Figure 3.1a,b). In addition, most interactions were also poorly supported overall, as well as being relatively rarely included in the top models, suggesting interactions have relatively little predictive power in these analyses. By contrast, phylogenetic logistic regression top model averaged weights

included all 13 terms in both Ericson and Hackett backbones, albeit very weakly in the case of many interactions (Figure 3.2a,b). The highest-weighted terms were Host, PC2 and PC3. Other well-supported predictors as judged by model weight include: PC2:PC3, and to a slightly lesser extent, PC1. In general model weight values were higher for phylogenetic logistic regression than for generalized linear models.

Parameter values were positive for Host in generalized linear model averages across trees in both backbones, suggesting support for Host as an important predictor of cooperative breeding (Figure 3.1c,d). Interestingly, we also found a strong *positive* effect of testis size in our averaged models, suggesting that while testis size is a good predictor, there is a positive rather than negative association between testis size and cooperative breeding. The ecological PCs are both weak in weight and inconsistent in their predictive direction, suggesting that they provide relatively less explanatory power for cooperative breeding. Phylogenetic logistic regression parameter values for top models also indicated a positive effect of parasite host status, but indicated a positive effect of PC2 and a negative effect of PC3 on the occurrence of cooperative breeding. The effect of PC2:PC3 was largely positive in these analyses, while PC1 was slightly positive (Figure 3.2c,d). Interestingly, the effect of testis size was generally positive: this is surprising, given that previous work using phylogenetic logistic regression to investigate Testis size as a univariate predictor of cooperative breeding gave uniformly negative associations between the two. Models containing only Testis size were indeed negative across all trees, but appear to switch to positive when additional covariates are included.

Regional analyses of cooperative breeding

For each of the five biogeographic regions (see methods), we ran each generalized linear model function using *dredge* for 90,000 iterations, discarding the first 10,000 iterations as a burn-in, and thinning chains every 150 iterations. Using *dredge*, we compared fit for 235 combinations of predictors of cooperative breeding (5 main predictors and 8 interactions).

Australia: For both phylogeny backbones, analyses based on most trees supported several models that were indistinguishable from the top model ($\Delta\text{AICc} < 2$) (Hackett mean: 4.3 models/tree; Ericson mean: 3.1 models/tree) (Appendix Table 3.4). Top model averaged weights were dominated by Testis, with no other potential covariate reaching a weight of over 0.50 (Figure 3.3b). The parameter value for Testis was positive, similar to generalized linear model globally but substantially larger in magnitude (Figure 3.3g).

Africa: Analyses of the African dataset recovered an average of 2.7 and 2.4 models per tree for the Ericson and Hackett backbones, respectively (Appendix Table 3.5). In a similar fashion to Australia, Africa's top model averaged weight was dominated by a single variable, but in this case Host. PC2 and PC3 had some weight, but neither surpassed 0.40 (Figure 3.3a). The model averaged parameter of Host was consistent in magnitude with global models, and PC3 was uniformly negative, suggesting a negative association between habitat heterogeneity and cooperative breeding (Figure 3.3f).

Nearctic: Analyses of species in the Nearctic region resulted in an average of 4.7 and 4.9 top models ($\Delta\text{AICc} \leq 2$) for the Ericson and Hackett backbone trees, respectively. PC1 dominated this biogeographic region's top model weights, and like other regions, no

other parameter contained weights above 0.40 (Figure 3.3c). PC1 was strongly positive, indicating a correlation between cooperative breeding and warm, moist environments (Figure 3.3h).

Neotropics: Analyses of Neotropical species resulted in an average of 4.1 and 3.9 top models ($\Delta\text{AICc} \leq 2$) per tree for Hackett and Ericson backbone trees, respectively. As in Africa, the highest weight for any parameter in the model-averaged top models was Host. However, PC3 and to a lesser extent Testis had slightly stronger support than Africa, with some models topping weights of 0.40 for each parameter (Figure 3.3d). The model averaged parameter value for Host was slightly higher than global generalized linear model values, while PC3 was weakly positive. Testis was nearly identical in sign and magnitude to global values (Figure 3.3j).

Palaearctic: Analyses of the Palaearctic species yielded an average of 6.7 and 6.8 models indistinguishable from the top model ($\Delta\text{AICc} \leq 2$) per tree for the Hackett and Ericson backbone trees, respectively (appendix Table 3.8). Somewhat surprisingly, but consistent with the other temperate region (Nearctic), the top model averaged weights were ecological variables, namely PC2 and PC1 (Figure 3.3e). Overall weights were lower in the Palaearctic, indicating weaker overall consensus among models and trees, with neither top weighted parameter above 0.60 top-model averaged weight. Parameter values from model averages show a strong positive association with PC1, again similar to the Nearctic results. However, PC2 is strongly negative, indicating a correlation between *high* precipitation predictability and cooperative breeding (Figure 3.3j).

DISCUSSION

Top models and model selection

In our global generalized linear model analyses, we found the three best supported models included just two predictors: status as a host of brood parasites and testis size. Neither the environmental components nor interactions among predictors were well supported as predictors. By contrast, phylogenetic logistic regression analyses favored models with heavy loadings for host status, environmental components PC1, PC2, and PC3, and an interaction between PC2 and PC3. Testis size was found to have a relatively weak contribution to the top models, generally with positive effects. Finally, model selection was critically dependent not only upon analytical approach, but also phylogenetic tree selection. Below, we discuss these results from the perspective of individual predictors and outline their implications for future comparative analyses of cooperative breeding

Brood parasitism consistently predicts cooperative breeding

In agreement with recent work (Feeney et al. 2013, Chapter 1) we found a highly weighted, strongly positive relationship between cooperative breeding and status as a host to avian brood parasites, regardless of analytical approach (Figure 3.1b,d; Figure 3.2b,d). Unfortunately, interpretation of this relationship is not straightforward: previous work by Wells and Barker (Chapter 1) suggests that this association could be a *result of* cooperative breeding, rather than a driver of it. Other authors (especially Feeney et al. (2013)) have argued that the increased fitness of larger groups in the presence of brood

parasites (at least one species) indicates cooperative breeding is an adaptive response to parasitism. In addition, given the scrutiny of breeding that has occurred in cooperative breeders, it is likely that most species recorded to be cooperative breeding have also been observed enough to determine the incidence of brood parasitism as well, which may not be the case for non-cooperative birds. Given that there is little previous work investigating the interactions between cooperative breeders and brood parasites, these findings call for additional work focused on brood parasitism's effect on fitness in cooperatively breeding species, as well as quantifying and matching the observational scrutiny of cooperative and non-cooperative species in future comparative studies.

Monogamy is not supported as a predictor of cooperative breeding

Overall, the results from our two global analyses appear to be nearly diametrically opposed: cooperative breeding in generalized linear mixed model analyses is heavily influenced by promiscuity (as measured by relative testis size) at a global scale (Figure 3.1b,d), while our logistic regression analyses suggest that promiscuity has a relatively weak role to play (Figure 3.2b,d). Coefficients for the effect of promiscuity included in the top models of both analyses were largely (but not completely, in the case of phylogenetic logistic regression) positive, by contrast with our expectation from all previous results (Cornwallis et al. 2010, Chapter 2). In phylogenetic logistic regression models, it appears that the addition of other parameters changes testis size from a negative predictor of cooperative breeding to a positive one. Our top model-averaged parameter estimates from both phylogenetic logistic regression and generalized linear model analyses suggest that while promiscuity may be an important predictor (and

significantly so in generalized linear model analyses), cooperative breeding is on average associated with *increased* promiscuity, contradicting expectations from the indirect benefits hypothesis.

If this positive relationship is not artefactual, it could be interpreted as reflecting a potential role for polyandry in the formation of cooperative groups, where a female mates with multiple adult males, recruiting them to help care for young (Piper and Slater 1993; Dunn et al. 1995; Whittingham et al. 1997; Webster et al. 2004). This would be consistent with some observations from *Campylorhynchus* wrens, where dispersal is female-biased and there is intense competition among females for vacant breeding positions in large groups (Zack and Rabenold 1989). There may also be a similar case in acorn woodpeckers (*Melanerpes formicivorus*), where both sexes compete to attain breeding status after one or both breeders die, and will attack members of the same sex attempting to fill the breeding position (Hannon et al. 1985; Koenig et al. 1998). Even so, many cooperative breeders currently exhibit genetic monogamy (Quinn et al. 1999; Warrington et al. 2013), which seems difficult to reconcile with this polyandry hypothesis. One potential way to do so involves group ontogeny. Specifically, cooperative polyandry or polygynandry could be important to the *establishment* of groups (perhaps as a way for females to accrue helpers), while later in the group's history, either intragroup competition among males (Mumme et al. 1983) or mother guarding effects of sons (Welbergen and Quader 2006) could limit the ability of the female breeder to pursue extra-pair mating, yielding monogamy. If this is the case, the positive effect of relative testis size may more accurately reflect the selective conditions tied to the origin of cooperative breeding, despite the subsequent development or evolution of monogamy in

some species. As research in cooperative breeding often targets populations with especially large or cooperative groups, this may misrepresent species means by undersampling groups in the early phases of formation, and oversampling well-established groups where mate guarding and mother guarding effects limit promiscuity.

Aseasonal environments are a weak predictor of cooperative breeding

The weight for PC1—for which higher values are associated with lack of seasonality—in generalized linear model analyses was low (mean top model-averaged weight=0), and the parameter values, while positive, were close to zero. For phylogenetic logistic regression, the variable was more heavily weighted (mean top model-averaged weight~0.8), but as in generalized linear model analyses, parameter values were close to zero, although slightly positive. Overall, while there is some support for aseasonality as a predictor of cooperative breeding, especially in logistic regression analyses, the association is fairly weak compared to other factors, and therefore we interpret this as poor support for the stable environments hypothesis. This finding suggests that although cooperative breeders are more likely to be tropical in distribution, warm, stable environments *per se* are not particularly important in the evolution of cooperative breeding.

The impact of precipitation uncertainty is supported in phylogenetic logistic regression, but not generalized linear models

Perhaps the greatest difference between the two analytical approaches used here was their contrasting results regarding the effect of precipitation uncertainty (PC2) on

cooperative breeding. In generalized linear model analyses, precipitation uncertainty was not strongly weighted (mean weight=0, Figure 3.1a,b). By contrast, logistic regression analyses weighted precipitation uncertainty higher than any factor other than host status (Figure 3.2a,b). In addition, the predictors for precipitation uncertainty were positively correlated (i.e. more uncertainty was associated with higher probability) with cooperative breeding in phylogenetic logistic regression, while the parameter estimates were not consistently positive or negative in generalized linear model analysis. Because it is unclear which analysis most accurately reconstructs the underlying relationship between cooperative breeding and precipitation uncertainty, we consider support for a bet-hedging explanation for cooperative breeding (Jetz and Rubenstein 2011; Rubenstein 2011) equivocal.

Habitat saturation does not appear to play a role in the evolution of cooperative breeding

While support across top models varied for PC3 (the environmental variable positively associated with habitat heterogeneity), with general linear model analysis weighting it the weakest among ecological interactions (Figure 3.1a,c), logistic regression ranked it third after host and PC2 (Figure 3.2a,c). However, while the model weights of this metric were different, the parameter estimate was not: PC3 trends towards negative values (although crossing zero) in general linear model analysis, and is largely negative in phylogenetic logistic regression analysis, suggesting that habitat for cooperative breeders tends to be more homogenous than non-cooperative species. Factors leading to habitat saturation are difficult to identify for a single species at a single location, let alone

for multiple species. Our measure of habitat heterogeneity—a proxy for limited optimal habitat—is crude, but provides a starting point for this difficult-to-quantify hypothesis. Overall, our findings argue against the habitat saturation hypothesis—albeit weakly—as an important factor for the evolution of cooperative breeding.

Interactions among predictors appear unimportant, with the exception of precipitation uncertainty and habitat heterogeneity

Both models had strikingly few interaction terms. This is surprising due to our *a priori* expectations that biotic and ecological factors would interact to drive the evolution of cooperation. Top models from our generalized linear model analyses included no interactions with appreciable weights, and while logistic regression found support for several interactions, they had fairly low model weight compared with the primary terms. The only interaction from either analysis that received substantial weight (weight >0.5) was the interaction between habitat heterogeneity and precipitation uncertainty (PC2:PC3) in logistic regression.

Regional analyses suggest differing temperate and tropical drivers

One of the most striking features of the regional models is the contrast between temperate biogeographic regions (Nearctic and Palearctic) and the tropical and sub-tropical regions (Africa, Australia, and the Neotropics). Analyses of temperate region data were consistently dominated by more ecological variables (e.g. the ecological PC's), while biotic variables (e.g. relative testis size, brood parasitism) tended to dominate analyses of species from the tropical and sub-tropical regions. Samples from the

temperate regions may have decreased power to infer drivers relative to those from tropical regions, due to lower proportional and total numbers both of all species and of cooperative breeders. This is reflected in the relatively larger numbers of top models per tree (4.7 and 6.7 in Nearctic and Palearctic, respectively), and greater disagreement across those models as to which predictors are most important. Even so, it is interesting that models from these two areas appear weighted towards abiotic variables, especially in contrast with other regions. One explanation for this pattern might lie in the increased importance in holding year-round territories in areas with major seasonal changes. Temperate birds are often migratory and therefore do not hold a territory long enough for offspring to accumulate, or overwintering mortality of neighboring conspecifics allows for dispersal of offspring in those that are sedentary (Graber and Graber 1979). In addition, high mortality in both overwintering and migratory birds may impose high penalties on waiting to reproduce. Taken together, these trends would then favor evolution of cooperative breeding in the warmest, most stable portions of the temperate zone, where turnover of territories is reduced and adult offspring can accrue on territories, as has been suggested previously (Arnold and Owens 1999). Indeed, we see such a pattern among Nearctic species, where the stable, warm PC1 is heavily favored for cooperative breeders in these ranges. This pattern also holds in the Palearctic, albeit in a less straightforward manner. Rather than being heavily weighted towards only PC1 with a positive association as the main model, cooperation in the Palearctic is also negatively associated with PC2 (precipitation uncertainty) and PC3 (habitat heterogeneity; Figure 3.3e). Results from both of these regions suggest an overall trend towards cooperation in warmer, more stable environments.

Although we found the tropical regions showed very different patterns from one another, in general cooperative breeding in tropical species appears to be better predicted by biotic rather than abiotic factors. Australia had testis size as the top predictor of cooperative breeding (although *high* promiscuity predicted cooperation, as in global models; Figure 3.3b). This finding suggests promiscuity is a major driver of cooperative breeding in Australia. This finding is surprising, given the expected importance of rainfall in changing resource availability in the largely arid continent (Jetz and Rubenstein 2011).

Cooperative breeding in both African and the Neotropical species was predicted most strongly by status as a host to brood parasites, and in the case of African lineages, this was the only factor with substantial (>0.20) model weight. This finding is not entirely surprising given the strong global and African regional correlations between cooperative breeding and brood parasitism (Feeney et al. 2013, Chapter 1). However, as discussed above, this result does not necessarily imply that brood parasitism imposes selection for sociality. In fact, finer-scale analyses in previous studies suggest that increased group sizes in cooperative breeders may attract parasites, rather than being a result of parasitism, as previously hypothesized (Chapter 1). Cooperative breeding in the Neotropics was secondarily influenced by both relative testis size—in line with generalized linear model global results—and PC3, both with positive effects (Figure 3.3d). Taken together, we found that cooperative breeding in each region appears to be correlated as much with local climatic and biotic conditions as with universally applicable predictors of sociality. It is possible that the size of biogeographic areas is still too crude to detect important regional effects, but the number of transitions to cooperative breeding may limit use of similar metrics at a finer geographic scale for all but the most

speciose of geographic regions. Overall, in the tropics the trend was towards biotic factors, especially brood parasitism, being better predictors of cooperative breeding than abiotic factors.

Discordance among comparative methods

Disturbingly, aside from strong support for a positive effect of hosting brood parasites on cooperation, the two analytical approaches (generalized linear mixed models and phylogenetic logistic regression) used here yielded little agreement regarding the best model. Between the two analyses, we find some support for *all* five primary climatic and biotic factors within our set of top models. The only significant parts of our global model that can be excluded are the importance of nearly all interactions: the interaction between precipitation uncertainty (PC2) and habitat heterogeneity (PC3) is the only interaction with appreciable model weight (and only in our logistic regression analyses). These results suggest that there are major effects of analysis choice on support for the predictors, and could to some degree explain why so many different individual factors have found support in previous analyses. Additionally, the change in effect direction for some factors, especially testis size, when combined with other factors in the logistic regression analyses suggests that the influence of other predictors in the model can profoundly affect the behavior of some factors, even without inclusion of interaction terms. However, while the *weight* of model components was highly variable, the coefficients of primary predictors (relative testis size, host status, and ecological components) generally had similar signs and magnitudes between both analyses,

suggesting estimates of predictors were relatively consistent (with the possible exceptions of testis size and PC2).

Unfortunately, we have no clear *a priori* expectation that one analytical approach is better than the other. While both methods are relatively new, MCMC analysis of generalized linear mixed models has been widely applied, and its implementation has been actively refined (Cornwallis et al. 2010; Hadfield 2010, 2015; Wagner et al. 2012; de Vos et al. 2014), while application of phylogenetic approaches to logistic regression problems is in its infancy and few such analyses have been published. However, phylogenetic logistic regression was developed specifically to address problems with the estimation of logistic regression with current comparative methods (Ives and Garland 2010). Simulation studies have found generalized mixed models and logistic regression should give similar fits (in terms of correctly identifying significant and non-significant predictors) with two continuous independent variables (Ives and Garland 2014), but to our knowledge, there have been no simulations with large numbers of predictors, or with a combination of binary and continuous predictors. In addition, while *predictor effects* in this simulation were similar, model selection outcomes with these methods were not addressed. A rigorous and well-controlled simulation study comparing the performance of these and other comparative methods with regard to accuracy, efficiency, and power would be useful in determining the best methods for data such as those analyzed here.

Tree topologies strongly influence results of comparative analyses

One important finding from the global analyses was the impact of the choice of phylogenetic tree on the top models ($\Delta\text{AICc} \leq 2$) favored. Analyses of the global dataset

supported anywhere from one to 19 equally-likely models depending on the specific posterior tree used in the analysis (Appendix Table 3.1, 3.2). Similar patterns were found in most regional analyses as well, with a range from 1-8 models in the African, Neotropical and Nearctic regions, 4 to 8 models in the Palearctic region, and 1-9 models in the Australian region. In trees for Australian species, the backbone used also had a pronounced effect on the likelihood of one of the top models: Host + PC2, which occurred as a top model in 80% of trees with the Hackett backbone and only 30% of trees with the Ericson backbone. While the estimated parameter values of predictors in a given model were generally uniform across the trees, the change in the ranking and relative weights of models is a disturbing finding, suggesting (not surprisingly) significant phylogenetic structuring of the variables analyzed here, that (perhaps more surprisingly) strongly affects the outcome of comparative analyses across all birds. This outcome dependency limits the utility of current species-level phylogenies for unambiguously identifying the best predictors of cooperative breeding in birds, and may have similar effects on analyses of other traits. The approach taken here has been to evaluate the variation in model support across phylogeny estimates, and report the factors that seem most uniformly favored regardless of topology. However, we have only included a relatively small number of trees; with the computationally-intensive comparative methods used here, it is not feasible to use the entire distribution of 10,000 trees, or even a substantial fraction of them. Even though some results appear consistent, it remains true that different trees (only one of which may be closest to the true relationships of these taxa—unless they are all equally bad) support conflicting sets of predictors. Inference of

a robustly-supported, fully data-based phylogeny of birds is necessary to resolve this issue.

Conversely, the large degree of divergence in the number and relative support of top models among trees highlights the importance of including phylogenetic history in comparative studies. Without a strong understanding of phylogenetic history, traits may be over- or underrepresented as important predictors of cooperative breeding. To date, with the exceptions of the correlation between brood parasitism and cooperative breeding by Feeney et al. (2012) and promiscuity by Cornwallis et al. (2010), none of the suggested predictors have been analyzed with phylogenetic history resolved to the species-level. While we are concerned by the divergence in models across trees, the inclusion of a clear, species-level hypothesis for shared evolutionary history is a critical component of comparative work, and attempting to perform such an analyses without adequately accounting for phylogeny may in fact mislead our identification of not only the best predictors but the ultimate causal agents in the evolution of cooperative breeding.

CONCLUSION

This work is the first time multiple hypothesized drivers of cooperative breeding in birds have had their relative importance assessed at a global and regional scale in a comparative framework. We found a strong, positive association with brood parasite host status in both models, suggesting that further work needs to be done on the role of brood parasitism in the evolution and maintenance of cooperative breeding (Feeney et al. 2013; Chapter 2). We found that neither the prediction of a negative association between

cooperative breeders and relative testis size nor the prediction of a positive correlation between habitat heterogeneity and cooperative breeding were supported, although each had high top-model averaged weights in generalized linear models and phylogenetic logistic regression analyses, respectively. We also encountered significant variation in the best-supported models across: 1) tree topologies, 2) analytical methods, and 3) biogeographic regions. Both tree topology and comparative method had a major influence on model selection, something both unexpected, and to our knowledge undescribed in the literature on large-scale comparative analyses. On one hand, these results emphasize the importance of integrating phylogenetic uncertainty into comparative analyses (as has widely been suggested (Huelsenbeck et al. 2000; Pagel and Lutzoni 2002; Freckleton 2009)) as well as the importance of reducing that uncertainty through better phylogenetic analysis. On the other hand, these results strongly suggest that further work on the relative performance of the comparative approaches used here is needed, so that the significance of conflicting results such as those obtained here can be evaluated and arbitrated.

Table 3.1—Loadings for the environmental principle components. Bolded loadings indicate substantial (loading >0.35) factors. PC1 is loaded with high predictability and high NPP, suggesting a warm environment with high NPP and predictable precipitation. PC2 is loaded most notably against predictable precipitation, and towards a heterogeneous habitat to a lesser extent. PC3 is loaded most heavily towards habit heterogeneity and to a lesser extent, predictable precipitation

PCA Loadings for Ecological Factors			
	PC1	PC2	PC3
PREDICTABILITY.PRECIP	0.1383798	-0.84985	0.431325
PREDICTABILITY.TEMP	0.394654	0.06283818	-0.166656
NPP	0.379273	0.04588837	0.2148024
HABITAT.HETEROGENEITY	-0.2897466	0.390178	0.730164
SQRT.MEAN.PRECIP	0.394473	0.05627635	0.3049755
SQRT.VAR.PRECIP	0.3687166	0.2815547	0.2932298
MEAN.TEMP.2	0.374656	0.19108939	-0.1064373
LN.VAR.TEMP	-0.406657	0.02251258	0.1287756

Figure 3.1 - Generalized linear models parameter weights and values for Ericson and Hackett Trees. All values are derived from the top models ($\Delta AIC_c < 2$) across a distribution of 100 trees. (a) model-averaged parameter weights for Hackett backbone trees. (b) Model-averaged parameter weights for Ericson backbone trees (c) model-averaged parameter values for Hackett backbone trees. (d) model-averaged parameter values for Ericson backbone trees

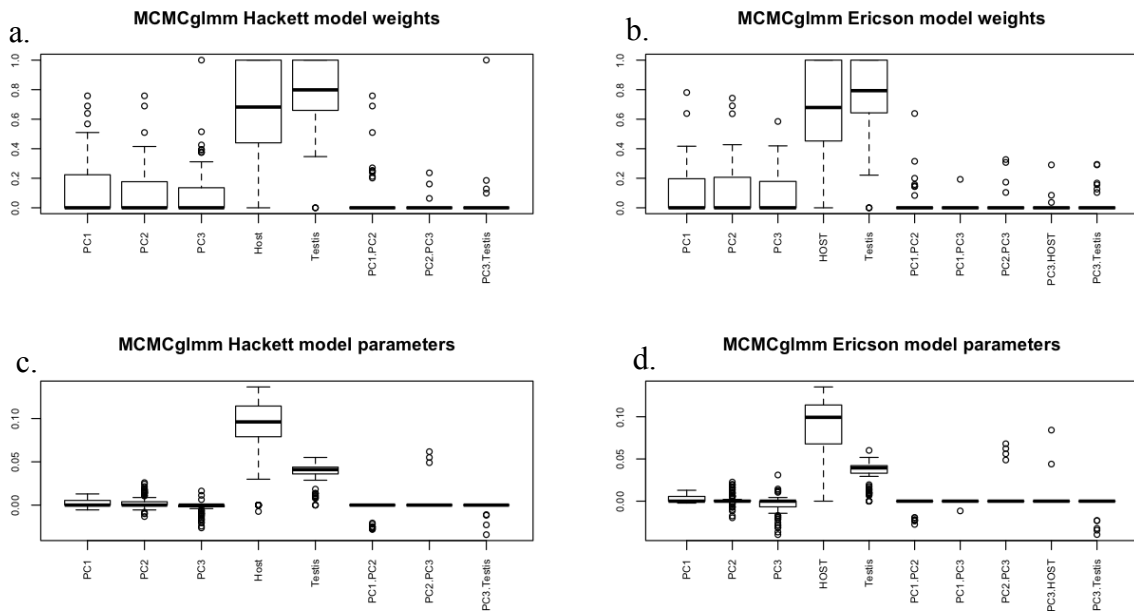


Figure 3.2 - Phylogenetic logistic regression results for Ericson and Hackett trees.

All values are derived from the top models ($\Delta AIC_c < 2$) across a distribution of 100 trees

(a) model-averaged parameter weights for Hackett backbone trees. (b) Model-averaged parameter weights for Ericson backbone trees (c) model-averaged parameter values for Hackett backbone trees. (d) model-averaged parameter values for Ericson backbone trees

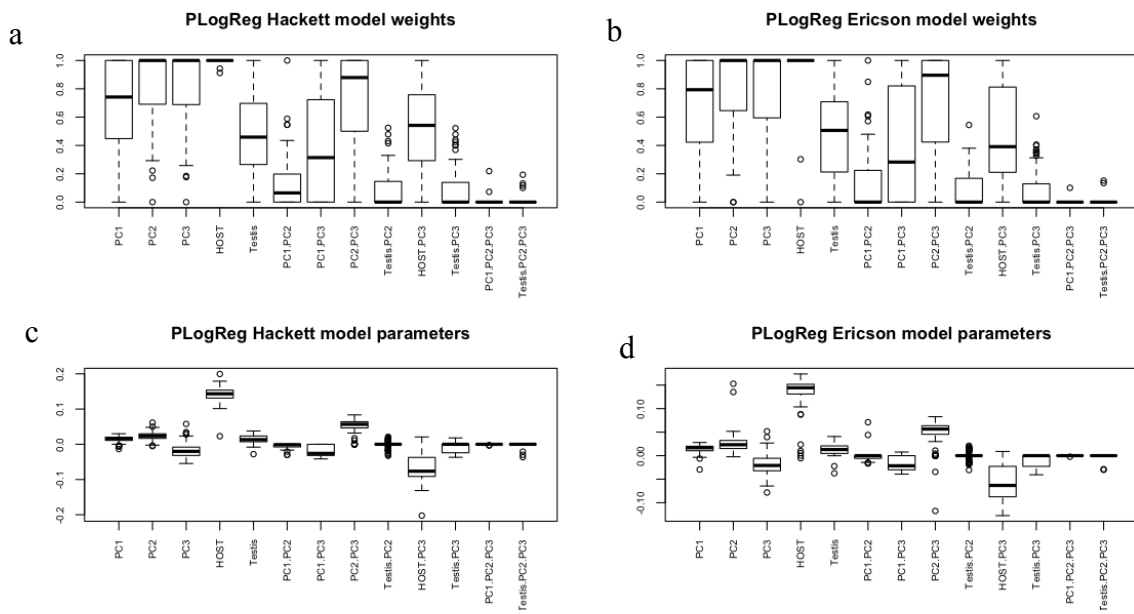
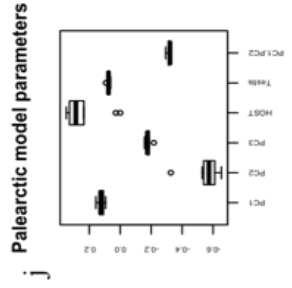
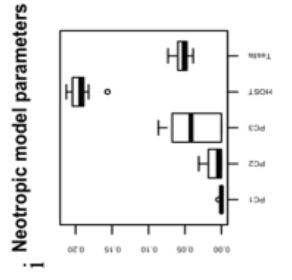
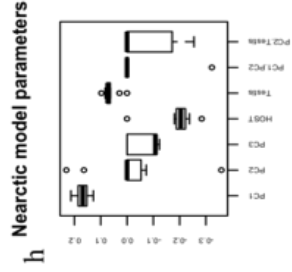
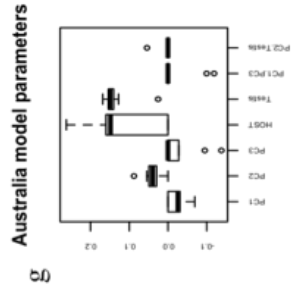
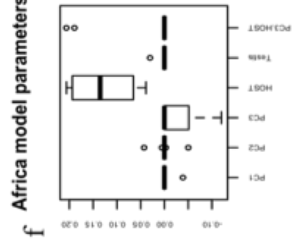
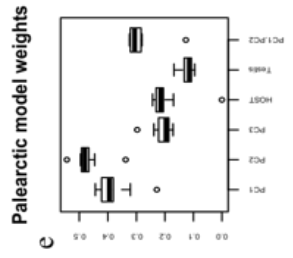
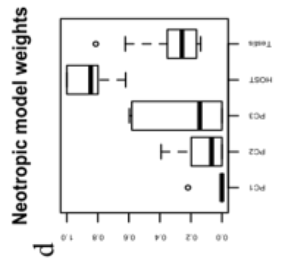
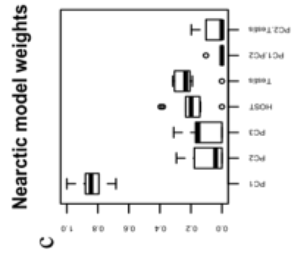
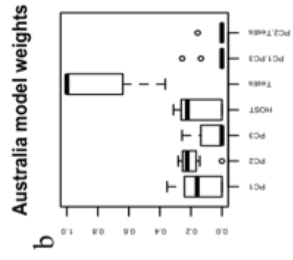
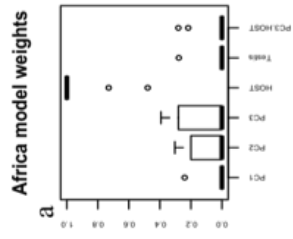


Figure 3.3 - Regional generalized linear models results. All results are derived from the top models ($\Delta AIC_c < 2$) from 10 trees in the Hackett backbone. Top row panels indicate top model parameter weights for each region, while bottom row panels indicate top model parameter estimates.



CONCLUSION

CONCLUSIONS AND WAYS FORWARD FOR STUDY COOPERATIVE BREEDING

This dissertation investigated at a global scale several potential drivers for the evolution of cooperative breeding (Chapters 1 and 2), and attempted to directly compare the importance and interaction of these and other potential drivers in a single analysis (Chapter 3).

In the first chapter, I found a strong positive correlation between cooperative breeding and brood parasitism, indicating a potential causal link. However, when I investigated transitions between the states of this correlation, I found that it was much more likely for the transition to brood parasitism to occur *after* the transition to cooperative breeding, rather than before the transition to cooperative breeding. This suggests that brood parasitism, rather than driving cooperative breeding, instead is a byproduct of parasite attraction to cooperative breeders.

In the second chapter, I investigated the expected negative correlation between cooperative breeding and promiscuity using relative testis size as a proxy. This proxy is easily obtained from museum collections, and compared to direct measures of promiscuity allows a larger and more unbiased sample. I found that in the first truly global sample, cooperative breeding shows a negative relationship with relative testis size, indicating support for previous findings that cooperative breeding preferentially evolves in monogamous lineages, in line with the hypothesis of indirect benefits as a driver for cooperative breeding behaviors.

Finally, I combined these factors as well as three ecological measures (warm, moist environments, precipitation uncertainty, and habitat heterogeneity) in order to determine their relative importance in predicting cooperative breeding across all birds. I found significantly different results, depending on the choice of analytical approach and on the specific phylogenetic trees used in the analyses. In both analyses, status as host to a brood parasite was highly favored as a predictor, and positively correlated with cooperative breeding, as in Chapter 1. In generalized linear mixed model analysis testis size joined parasitism as an important factor, but was *positively* associated with cooperative breeding, suggesting that promiscuity rather than monogamy favored cooperative breeding. By contrast, phylogenetic logistic regression favored environmental factors, especially increased precipitation uncertainty and low habitat heterogeneity as the best predictors of cooperative breeding. These results starkly illustrate there are still considerable hurdles to overcome in the data and methodology before we can begin to understand the ultimate or regional driver or drivers of cooperative breeding in birds.

While better methodology and improved estimates of phylogeny will undoubtedly allow improvements in the analysis of data, there is also considerable room for improvement in the type and quality of the comparative data used. Foremost, as analyzed here cooperative breeding was a broadly defined categorical trait. However, cooperative breeding is a complex suite of behaviors that are superficially similar, but have almost certainly been derived from independent origins and are most certainly convergent. The choice to reduce this complexity to a binary character has at least two problems associated with it. First, it means that a significant amount of data regarding details of the

group size distributions within species is lost. Second, and possibly more importantly, a binary designation lumps together a large amount of variation in the underlying social system such as the likelihood of having helpers, reproductive skew within the group and any regional differences within species. In addition, this coding also misses potentially important transitional behaviors, such as extended parental care (Drobniak et al. 2015), which could be a crucial intermediary step in the evolution of cooperative breeding. Finally, the underlying social system of these different species can be radically different. For instance, three of the best-studied cooperative species, Acorn woodpeckers, Florida scrub-jays, and fairy wrens all differ in the levels of monogamy, the numbers of sexually active animals in a group, and group size (Koenig and Stacey 1990). Finding some way to account for both the similarities and differences among these groups would make it clear that we are both making comparisons among groups with similar attributes, and therefore potentially similar evolutionary pressures, and ensuring we are not lumping several subtypes of sociality together, which could cancel drivers out, or produce spurious correlations. Some work has been started on non-cooperative groups using the length of post-fledgling care (Drobniak et al. 2015). Extending this to cooperative breeding, or combining this with other factors, could be a useful way forward. Another possible way forward is to broaden samples of cooperatively breeding species (below). Shifting cooperative breeding from a binary to a Poisson trait, or splitting the overarching concept of cooperative breeding into several distinct social systems as a multi-state trait may help alleviate some of the discordant results we have found here.

This global study also highlights a different problem with past and current approaches to the study cooperative breeding: they generally follow one of two major

approaches (but see Koenig and Stacey (1990) for a notable exception). The first, and oldest, approach is the detailed, longitudinal study of a small number of groups, generally in a geographically restricted area to facilitate better observation and gathering of demographic data. Individuals are generally individually marked and are followed for years. In this way, recruitment, reproductive success, relatedness and transitions from helper to breeder can be elucidated in great detail. The drawback of this approach stems from the cost and manpower required for this endeavor: relatively few groups can be covered, and the few groups that are covered are often from a geographically restricted area. In addition, the choice of groups to be followed often is biased to the largest groups in the area, potentially biasing studies toward unusual circumstances that increase the group size above normal. Finally, in-depth, single species studies focus on only one evolutionary lineage—this means it is difficult to separate lineage-specific idiosyncrasies from the true general drivers of cooperative breeding. Thus, depth of understanding is attained at local scales, but at the cost of generality.

The second approach, which is the focus of this dissertation, is the use of large data sets to explore the global correlations across cooperative breeding. Global studies take advantage of more coarse-grained data to attain larger sample sizes, phylogenetic breadth, and greater variation in environment and biological factors in order to investigate sociality on a macroevolutionary scale. Aside from phylogenetic and methodological drawbacks reported in the third chapter of this thesis, global studies are extremely reliant on published information, with great variance in the quality of observations. For instance, while well-studied cooperative breeders are clearly social, there are many species that are considered cooperative from only a few observations at a

single location. While these may well be valid for the species, the observers may have also mistaken a rare event for a common one. In addition, predictors generally use the species means or medians as the value for global analysis. These choices make it straightforward to calculate these predictors. However, if there is a difference in population or species level tendencies towards cooperative breeding, we are ignoring potentially very valuable information on how ecology affects cooperative breeding. This in turn brings up the same weakness shared between global studies and local, in-depth studies: the problem of regional or species-level variability on the trait of cooperative breeding. For instance, investigations of acorn woodpecker populations in California, Arizona and New Mexico found that populations in the more arid New Mexico and Arizona were far less likely to form cooperatively breeding groups, and when groups did form, they had a smaller maximum size than the California population (Koenig and Stacey 1990).

Future studies might be best served by taking a middle route between the in-depth, geographically restricted analyses and large, superficial global analyses. Careful regional or species-level inventories of the proportion of populations that are cooperatively breeding could be very informative, especially if several independent lineages could be assessed in similar ecological conditions. This would allow a more continuous measure of cooperative breeding (group size, or proportion of territories with cooperative breeders), as well as allow for gathering finer-scale data on the coincidence of explanatory factors and the strength of cooperation (e.g. being able to regress group size on ecological factors through an ecological continuum). From the perspective of an in-depth project, these data come at cost of accuracy: for instance, the exact number of

birds in the group is difficult to determine without individual marking, which is incredibly labor-intensive. However, if carefully designed (e.g. to avoid counting fledglings) and composed of multiple, independently-evolved lineages and having a similar social system, broad regional- and species-level surveys could be a powerful tool to understand how ecological and demographic gradients may affect cooperative breeding, and help break through the impasse regarding causal inference we currently suffer.

BIBLIOGRAPHY

- Aragon, S., A. P. Moller, J. J. Soler, and M. Soler. 1999. Molecular phylogeny of cuckoos supports a polyphyletic origin of brood parasitism. *J. Evol. Biol.* 12:495–506.
- Arnold, K. E., and I. P. Owens. 1999. Cooperative breeding in birds: the role of ecology. *Behav. Ecol.* 10:465–471.
- Barker, F. K., K. J. Burns, J. Klicka, S. M. Lanyon, and I. J. Lovette. 2015. New insights into New World biogeography: An integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. *The Auk* 132:333–348.
- Barton, K. 2013. MuMIn: Multi-model inference. R Package Version 195.
- Botero, C. A., R. Dor, C. M. McCain, and R. J. Safran. 2014. Environmental harshness is positively correlated with intraspecific divergence in mammals and birds. *Mol. Ecol.* 23:259–268.
- Briskie, J. V., and R. Montgomerie. 1992. Sperm Size and Sperm Competition in Birds. *Proc. R. Soc. Lond. B Biol. Sci.* 247:89–95.
- Brown, J. L. 1987. *Helping Communal Breeding in Birds: Ecology and Evolution.* Princeton University Press.
- Calhim, S., and T. R. Birkhead. 2007. Testes size in birds: quality versus quantity—assumptions, errors, and estimates. *Behav. Ecol.* 18:271–275.
- Calhim, S., and R. Montgomerie. 2015. Testis asymmetry in birds: the influences of sexual and natural selection. *J. Avian Biol.* 46:175–185.
- Canestrari, D., J. M. Marcos, and V. Baglione. 2009. Cooperative breeding in carrion crows reduces the rate of brood parasitism by great spotted cuckoos. *Anim. Behav.* 77:1337–1344.
- Cardinal, S., and B. N. Danforth. 2011. The antiquity and evolutionary history of social behavior in bees. *PLoS One* 6:e21086.
- Cheng, T. L., S. M. Rovito, D. B. Wake, and V. T. Vredenburg. 2011. Coincident mass extirpation of neotropical amphibians with the emergence of the infectious fungal pathogen *Batrachochytrium dendrobatidis*. *Proc. Natl. Acad. Sci.* 108:9502–9507.
- Clutton-Brock, T. 2002. *Breeding Together: Kin Selection and Mutualism in Cooperative Vertebrates.* Science 296:69–72.
- Clutton-Brock, T. 2009. Cooperation between non-kin in animal societies. *Nature* 462:51–57.

- Clutton-Brock, T. H., D. Gaynor, G. M. McIlrath, A. D. C. Maccoll, R. Kansky, P. Chadwick, M. Manser, J. D. Skinner, and P. N. M. Brotherton. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *J. Anim. Ecol.* 68:672–683.
- Cockburn, A. 2003. Cooperative breeding in oscine passerines: does sociality inhibit speciation? *Proc. R. Soc. Lond. B Biol. Sci.* 270:2207–2214.
- Cockburn, A. 2006. Prevalence of different modes of parental care in birds. *Proc. R. Soc. B Biol. Sci.* 273:1375–1383.
- Constable, H., R. Guralnick, J. Wiczorek, C. Spencer, A. T. Peterson, and The VertNet Steering Committee. 2010. VertNet: A New Model for Biodiversity Data Sharing. *PLoS Biol* 8:e1000309.
- Cornwallis, C. K., S. A. West, K. E. Davis, and A. S. Griffin. 2010. Promiscuity and the evolutionary transition to complex societies. *Nature* 466:969–972.
- Darwin, C. R. 1859. *On the origin of species by means of natural selection, or the Preservation of favoured races in the struggle for life.*
- Davies, N. B. 1985. Cooperation and conflict among dunnocks, *Prunella modularis*, in a variable mating system. *Anim. Behav.* 33:628–648.
- Davies, N. B. 2000. *Cuckoos, Cowbirds and Other Cheats.* (T. and AD Poyser: London.).
- Dearborn, D. C. 1999. Brown-headed cowbird nestling vocalizations and risk of nest predation. *The Auk* 448–457.
- de Vos, J. M., R. O. Wüest, and E. Conti. 2014. Small and Ugly? Phylogenetic Analyses of the “selfing Syndrome” Reveal Complex Evolutionary Fates of Monomorphic Primrose Flowers. *Evolution* 68:1042–1057.
- Drobniak, S. M., G. Wagner, E. Mourocq, and M. Griesser. 2015. Family living: an overlooked but pivotal social system to understand the evolution of cooperative breeding. *Behav. Ecol. arv015.*
- Dunn, P. O., A. Cockburn, and R. A. Mulder. 1995. Fairy-Wren Helpers often Care for Young to Which they are Unrelated. *Proc. R. Soc. Lond. B Biol. Sci.* 259:339–343.
- Edwards, S. V., and S. Naeem. 1993. The phylogenetic component of cooperative breeding in perching birds. *Am. Nat.* 754–789.
- Emlen, S. T. 1982. The Evolution of Helping. I. An Ecological Constraints Model. *Am. Nat.* 119:29–39.
- Ericson, P. G. P., D. Zuccon, J. I. Ohlson, U. S. Johansson, H. Alvarenga, and R. O. Prum. 2006. Higher-level phylogeny and morphological evolution of tyrant flycatchers,

- cotingas, manakins, and their allies (Aves: Tyrannida). *Mol. Phylogenet. Evol.* 40:471–483.
- Evans, H. E. 1977. Commentary: extrinsic versus intrinsic factors in the evolution of insect sociality. *Bioscience* 27:613–617.
- Feeney, W. E., I. Medina, M. Somveille, R. Heinsohn, M. L. Hall, R. A. Mulder, J. A. Stein, R. M. Kilner, and N. E. Langmore. 2013. Brood Parasitism and the Evolution of Cooperative Breeding in Birds. *science* 342:1506–1508.
- Fisher, D. O., C. R. Dickman, M. E. Jones, and S. P. Blomberg. 2013. Sperm competition drives the evolution of suicidal reproduction in mammals. *Proc. Natl. Acad. Sci.* 110:17910–17914.
- Fisher, H. S., and H. E. Hoekstra. 2010. Competition drives cooperation among closely related sperm of deer mice. *Nature* 463:801–803.
- Freckleton, R. P. 2009. The seven deadly sins of comparative analysis. *J. Evol. Biol.* 22:1367–1375.
- Friedmann, H. 1955. *The honey-guides*. Smithsonian Institution Washington, DC.
- Friedmann, H. 1960. *The parasitic weaverbirds*. Smithsonian Institution.
- Fry, C. H. 1972. *The Social Organisation of Bee-Eaters (meropidae) and Co-Operative Breeding in Hot-Climature Birds*. *Ibis* 114:1–14.
- Gibbs, H. L., P. J. Weatherhead, P. T. Boag, B. N. White, L. M. Tabak, and D. J. Hoysak. 1990. Realized Reproductive Success of Polygynous Red-Winged Blackbirds Revealed by DNA Markers. *Science* 250:1394–1397.
- Gilchrist, J. S. 2004. Pup escorting in the communal breeding banded mongoose: behavior, benefits, and maintenance. *Behav. Ecol.* 15:952–960.
- Gomendio, M., and E. R. S. Roldan. 1991. Sperm Competition Influences Sperm Size in Mammals. *Proc. R. Soc. Lond. B Biol. Sci.* 243:181–185.
- Gonzalez, J.-C. T., B. C. Sheldon, and J. A. Tobias. 2013. Environmental stability and the evolution of cooperative breeding in hornbills. *Proc. R. Soc. B Biol. Sci.* 280:20131297.
- Graber, J. W., and R. R. Graber. 1979. Severe Winter Weather and Bird Populations in Southern Illinois. *Wilson Bull.* 91:88–103.
- Graw, B., and M. B. Manser. 2007. The function of mobbing in cooperative meerkats. *Anim. Behav.* 74:507–517.
- Gross, M. R., and E. L. Charnov. 1980. Alternative male life histories in bluegill sunfish. *Proc. Natl. Acad. Sci.* 77:6937–6940.

- Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, W. A. Cox, K.-L. Han, J. Harshman, C. J. Huddleston, B. D. Marks, K. J. Miglia, W. S. Moore, F. H. Sheldon, D. W. Steadman, C. C. Witt, and T. Yuri. 2008. A Phylogenomic Study of Birds Reveals Their Evolutionary History. *Science* 320:1763–1768.
- Hadfield, J. D. 2015. Increasing the efficiency of MCMC for hierarchical phylogenetic models of categorical traits using reduced mixed models. *Methods Ecol. Evol.* 6:706–714.
- Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* 33:1–22.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour. I. *J. Theor. Biol.* 7:1–16.
- Hannon, S. J., R. L. Mumme, W. D. Koenig, and F. A. Pitelka. 1985. Replacement of breeders and within-group conflict in the cooperatively breeding acorn woodpecker. *Behav. Ecol. Sociobiol.* 17:303–312.
- Harcourt, A. H., A. Purvis, and L. Liles. 1995. Sperm Competition: Mating System, Not Breeding Season, Affects Testes Size of Primates. *Funct. Ecol.* 9:468–476.
- Hatchwell, B. J. 2009. The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philos. Trans. R. Soc. B Biol. Sci.* 364:3217–3227.
- Hatchwell, B. J., and J. Komdeur. 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Anim. Behav.* 59:1079–1086.
- Heinsohn, R. G. 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *Am. Nat.* 864–881.
- Hill, K., and A. M. Hurtado. 2009. Cooperative breeding in South American hunter-gatherers. *Proc. R. Soc. B Biol. Sci.* rspb20091061.
- Ho, L.S.T., and C. Ane. 2014. Package “Phylolm”- Phylogenetic Linear Regression.
- Hogendoorn, K., and J. Zammit. 2001. Benefits of cooperative breeding through increased colony survival in an allodapine bee. *Insectes Sociaux* 48:392–397.
- Hoover, J. P., and M. J. Reetz. 2006. Brood parasitism increases provisioning rate, and reduces offspring recruitment and adult return rates, in a cowbird host. *Oecologia* 149:165–173.
- Hrdy, S. 2007. *Family Relationships : An Evolutionary Perspective: An Evolutionary Perspective.* Oxford University Press, USA.

- Huelsenbeck, J. P., B. Rannala, and J. P. Masly. 2000. Accommodating Phylogenetic Uncertainty in Evolutionary Studies. *Science* 288:2349–2350.
- Ives, A. R., and T. Garland. 2010. Phylogenetic Logistic Regression for Binary Dependent Variables. *Syst. Biol.* 59:9–26.
- Ives, A. R., and T. G. Garland. 2014. Phylogenetic Regression for Binary Dependent Variables. Pp. 231–261 *in* L. Z. Garamszegi, ed. *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*. Springer Berlin Heidelberg.
- Jetz, W., and D. R. Rubenstein. 2011. Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.* 21:72–78.
- Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. *Nature* 491:444–448.
- John Maynard Smith. 1995. *The major transitions in evolution*. WHFreeman Spektrum, Oxford ; New York.
- Judd, T. M. 1998. Defensive behavior of colonies of the paper wasp, *Polistes fuscatus*, against vertebrate predators over the colony cycle. *Insectes Sociaux* 45:197–208.
- Kass, R. E., and A. E. Raftery. 1995. Bayes factors. *J. Am. Stat. Assoc.* 90:773–795.
- Keith, S., E. K. Urban, and C. H. Fry. 2000. *The birds of Africa*. Academic Press.
- Kilner, R. M., D. G. Noble, and N. B. Davies. 1999. Signals of need in parent–offspring communication and their exploitation by the common cuckoo. *Nature* 397:667–672.
- Koenig, W. D., and J. L. Dickinson. 2004. *Ecology and evolution of cooperative breeding in birds*. Cambridge University Press.
- Koenig, W. D., J. Haydock, and M. T. Stanback. 1998. Reproductive Roles in the Cooperatively Breeding Acorn Woodpecker: Incest Avoidance versus Reproductive Competition. *Am. Nat.* 151:243–255.
- Koenig, W. D., and P. B. Stacey. 1990. Acorn woodpeckers: group-living and food storage under contrasting ecological conditions. *Coop. Breed. Birds* 415–453.
- Komdeur, J., A. Huffstadt, W. Prast, G. Castle, R. Mileto, and J. Wattel. 1995. Transfer experiments of Seychelles warblers to new islands: changes in dispersal and helping behaviour. *Anim. Behav.* 49:695–708.
- Lanyon, S. M. 1992. Interspecific brood parasitism in blackbirds(Icterinae): A phylogenetic perspective. *Science.* 255:77–79.

- Laskemoen, T., O. Kleven, F. Fossøy, R. J. Robertson, G. Rudolfson, and J. T. Lifjeld. 2010. Sperm quantity and quality effects on fertilization success in a highly promiscuous passerine, the tree swallow *Tachycineta bicolor*. *Behav. Ecol. Sociobiol.* 64:1473–1483.
- Lennartz, M. R., R. G. Hooper, and R. F. Harlow. 1987. Sociality and cooperative breeding of red-cockaded woodpeckers, *Picoides borealis*. *Behav. Ecol. Sociobiol.* 20:77–88.
- Ligon, J. D., and D. B. Burt. 2004. 1• Evolutionary origins. *Ecol. Evol. Coop. Breed. Birds* 5.
- Ligon, J. D., and S. H. Ligon. 1990. Green woodhoopoes: life history traits and sociality. *Coop. Breed. Birds Camb. Univ. Press Camb.* 31:66.
- Lin, N., and C. D. Michener. 1972. Evolution of Sociality in Insects. *Q. Rev. Biol.* 47:131–159.
- Liu, Y., J. T. Curtis, and Z. Wang. 2001. Vasopressin in the lateral septum regulates pair bond formation in male prairie voles (*Microtus ochrogaster*). *Behav. Neurosci.* 115:910–919.
- Lowther, P.E. 2012 <https://www.fieldmuseum.org/science/blog/brood-parasitism-host-lists>
- Lüpold, S., G. M. Linz, J. W. Rivers, D. F. Westneat, and T. R. Birkhead. 2009. Sperm Competition Selects Beyond Relative Testes Size in Birds. *Evolution* 63:391–402.
- Menaker, M., and H. Keatts. 1968. Extraretinal light perception in the sparrow. II. Photoperiodic stimulation of testis growth. *Proc. Natl. Acad. Sci. U. S. A.* 60:146–151.
- Mitra, S., H. Landel, and S. Pruett-Jones. 1996. Species Richness Covaries with Mating System in Birds. *The Auk* 113:544–551.
- Moksnes, A., and E. Røskoft. 1995. Egg-morphs and host preference in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *J. Zool.* 236:625–648.
- Møller, A. P. 1988. Ejaculate quality, testes size and sperm competition in primates. *J. Hum. Evol.* 17:479–488.
- Moller, A. P. 1989. Ejaculate Quality, Testes Size and Sperm Production in Mammals. *Funct. Ecol.* 3:91–96.
- Moller, A. P. 1991. Sperm Competition, Sperm Depletion, Paternal Care, and Relative Testis Size in Birds. *Am. Nat.* 137:882–906.
- Moller, A. P., and J. V. Briskie. 1995. Extra-pair paternity, sperm competition and the evolution of testis size in birds. *Behav. Ecol. Sociobiol.* 36:357–365.

- Mulder, R. A., P. O. Dunn, A. Cockburn, K. A. Lazenby-Cohen, and M. J. Howell. 1994. Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. *Proc. Biol. Sci.* 223–229.
- Mumme, R. L. 1992. Do helpers increase reproductive success? *Behav. Ecol. Sociobiol.* 31:319–328.
- Mumme, R. L., W. D. Koenig, and F. A. Pitelka. 1983. Mate guarding in the acorn woodpecker: Within-group reproductive competition in a cooperative breeder. *Anim. Behav.* 31:1094–1106.
- Neff, B. D. 2003. Decisions about parental care in response to perceived paternity. *Nature* 422:716–719.
- Neff, B. D., and M. R. Gross. 2001. Dynamic adjustment of parental care in response to perceived paternity. *Proc. R. Soc. Lond. B Biol. Sci.* 268:1559–1565.
- Nowak, M. A., C. E. Tarnita, and E. O. Wilson. 2010. The evolution of eusociality. *Nature* 466:1057–1062.
- Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D’amico, I. Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettengel, P. Hedao, and K. R. Kassem. 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 51:933–938.
- Pagel, M., and F. Lutzoni. 2002. Accounting for phylogenetic uncertainty in comparative studies of evolution and adaptation. Pp. 148–161 *in* M. Lässig and A. Valleriani, eds. *Biological Evolution and Statistical Physics*. Springer Berlin Heidelberg.
- Pagel, M., and A. Meade. 2006. Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *Am. Nat.* 167:808–825.
- Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics* 20:289–290.
- Payne, R. B. 2005. *The cuckoos*. Oxford University Press.
- Piper, W. H., and G. Slater. 1993. Polyandry and Incest Avoidance in the Cooperative Stripe-Backed Wren of Venezuela. *Behaviour* 124:227–247.
- Pizzari, T., C. K. Cornwallis, H. Løvlie, S. Jakobsson, and T. R. Birkhead. 2003. Sophisticated sperm allocation in male fowl. *Nature* 426:70–74.
- Plessis, M. A. D. 1992. Obligate cavity-roosting as a constraint on dispersal of green (red-billed) woodhoopoes: consequences for philopatry and the likelihood of inbreeding. *Oecologia* 90:205–211.

- Poiani, A., and M. A. Elgar. 1994. Cooperative breeding in the Australian avifauna and brood parasitism by cuckoos (Cuculidae). *Anim. Behav.* 47:697–706.
- Powell, A. F., F. K. Barker, S. M. Lanyon, K. J. Burns, J. Klicka, and I. J. Lovette. 2014. A comprehensive species-level molecular phylogeny of the New World blackbirds (Icteridae). *Mol. Phylogenet. Evol.* 71:94–112.
- Preston, B. T., I. R. Stevenson, J. M. Pemberton, D. W. Coltman, and K. Wilson. 2003. Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. *Proc. R. Soc. Lond. B Biol. Sci.* 270:633–640.
- Quinn, J. S., G. E. Woolfenden, J. W. Fitzpatrick, and B. N. White. 1999. Multi-locus DNA fingerprinting supports genetic monogamy in Florida scrub-jays. *Behav. Ecol. Sociobiol.* 45:1–10.
- Rabosky, D. L., F. Santini, J. Eastman, S. A. Smith, B. Sidlauskas, J. Chang, and M. E. Alfaro. 2013. Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nat. Commun.* 4.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
- Restrepo, C., and M. L. Mondragón. 1998. Cooperative Breeding in the Frugivorous Toucan Barbet (*Semnornis ramphastinus*). *The Auk* 115:4–15.
- Ricklefs, R. E., and M. Pagel. 2012. Evolutionary biology: Birds of a feather. *Nature* 491:336–337.
- Riehl, C. 2012. Mating system and reproductive skew in a communally breeding cuckoo: hard-working males do not sire more young. *Anim. Behav.* 84:707–714.
- Rubenstein, D. R. 2007. Female extrapair mate choice in a cooperative breeder: trading sex for help and increasing offspring heterozygosity. *Proc. R. Soc. Lond. B Biol. Sci.* 274:1895–1903.
- Rubenstein, D. R. 2011. Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proc. Natl. Acad. Sci.* 108:10816–10822.
- Rubenstein, D. R., and I. J. Lovette. 2007. Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.* 17:1414–1419.
- Shaffer, H. B., R. N. Fisher, and C. Davidson. 1998. The role of natural history collections in documenting species declines. *Trends Ecol. Evol.* 13:27–30.
- Skutch, A. F. 1935. Helpers at the nest. *The Auk* 257–273.

- Snell-Rood, E. C., and N. Wick. 2013. Anthropogenic environments exert variable selection on cranial capacity in mammals. *Proc. R. Soc. Lond. B Biol. Sci.* 280:20131384.
- Solomon, N. G., and J. A. French. 1997. *Cooperative Breeding in Mammals*. Cambridge University Press.
- Sorenson, M. D., and R. B. Payne. 2001. A SINGLE ANCIENT ORIGIN OF BROOD PARASITISM IN AFRICAN FINCHES: IMPLICATIONS FOR HOST-PARASITE COEVOLUTION. *Evolution* 55:2550–2567.
- Sorenson, M. D., R. B. Payne, and R. B. Payne. 2005. A molecular genetic analysis of cuckoo phylogeny. *Cuckoos Oxf. Univ. Press Oxf.* 68–94.
- Spottiswoode, C. N., K. F. Stryjewski, S. Quader, J. F. R. Colebrook-Robjent, and M. D. Sorenson. 2011. Ancient host specificity within a single species of brood parasitic bird. *Proc. Natl. Acad. Sci.* 108:17738–17742.
- Stacey, P. B., and W. D. Koenig. 1990. *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge University Press Cambridge, United Kingdom.
- Stephens, D. W., C. M. McLinn, and J. R. Stevens. 2002. Discounting and reciprocity in an iterated prisoner's dilemma. *Science* 298:2216–2218.
- Stockley, P., M. J. G. Gage, A. Parker G., and A. P. Møller. 1997. Sperm Competition in Fishes: The Evolution of Testis Size and Ejaculate Characteristics. *Am. Nat.* 149:933–954.
- Stürup, M., B. Baer, and J. J. Boomsma. 2014. Short independent lives and selection for maximal sperm survival make investment in immune defences unprofitable for leaf-cutting ant males. *Behav. Ecol. Sociobiol.* 68:947–955.
- Stutchbury, B.J., and E.S. Morton. 2001. *Behavioral Ecology of Tropical Birds*.
- Suarez, A. V., and N. D. Tsutsui. 2004. The Value of Museum Collections for Research and Society. *BioScience* 54:66–74.
- Sue Carter, C., A. Courtney Devries, and L. L. Getz. 1995. Physiological substrates of mammalian monogamy: The prairie vole model. *Neurosci. Biobehav. Rev.* 19:303–314.
- Tanaka, K. D., and K. Ueda. 2005. Horsfield's Hawk-Cuckoo Nestlings Simulate Multiple Gapes for Begging. *Science* 308:653–653.
- Tjur, T. 2009. Coefficients of Determination in Logistic Regression Models—A New Proposal: The Coefficient of Discrimination. *Am. Stat.* 63:366–372.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 35–57.

- Vehrencamp, S. L. 1978. The adaptive significance of communal nesting in Groove-billed anis (*Crotophaga sulcirostris*). *Behav. Ecol. Sociobiol.* 4:1–33.
- Wagner, C. E., L. J. Harmon, and O. Seehausen. 2012. Ecological opportunity and sexual selection together predict adaptive radiation. *Nature* 487:366–369.
- Walters, J. R., C. K. Copeyon, and J. H. Carter III. 1992. Test of the Ecological Basis of Cooperative Breeding in Red-Cockaded Woodpeckers. *The Auk* 109:90–97.
- Warrington, M. H., L. A. Rollins, N. J. Raihani, A. F. Russell, and S. C. Griffith. 2013. Genetic monogamy despite variable ecological conditions and social environment in the cooperatively breeding apostlebird. *Ecol. Evol.* 3:4669–4682.
- Webster, M. S., K. A. Tarvin, E. M. Tuttle, and S. Pruett-Jones. 2004. Reproductive promiscuity in the splendid fairy-wren: effects of group size and auxiliary reproduction. *Behav. Ecol.* 15:907–915.
- Welbergen, J. A., and S. Quader. 2006. Mother guarding: how offspring may influence the extra-pair behaviour of their parents. *Proc. R. Soc. Lond. B Biol. Sci.* 273:2363–2368.
- Whittingham, L. A., P. O. Dunn, and R. D. Magrath. 1997. Relatedness, polyandry and extra-group paternity in the cooperatively-breeding white-browed scrubwren (*Sericornis frontalis*). *Behav. Ecol. Sociobiol.* 40:261–270.
- Wiley, R. H., and K. N. Rabenold. 1984. The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. *Evolution* 609–621.
- Wilkinson, G. S. 1984. Reciprocal food sharing in the vampire bat. *Nature* 308:181–184.
- Wilkinson, R. 1982. Social organization and communal breeding in the chestnut-bellied starling (*Spreo pulcher*). *Anim. Behav.* 30:1118–1128.
- Wilson, E. O., and B. Hölldobler. 2005. Eusociality: Origin and consequences. *Proc. Natl. Acad. Sci. U. S. A.* 102:13367–13371.
- Wong, M., and S. Balshine. 2011. The evolution of cooperative breeding in the African cichlid fish, *Neolamprologus pulcher*. *Biol. Rev.* 86:511–530.
- Zack, S., and K. N. Rabenold. 1989. Assessment, age and proximity in dispersal contests among cooperative wrens: field experiments. *Anim. Behav.* 38:235–247.
- Zuk, M., J. D. Ligon, and R. Thornhill. 1992. Effects of experimental manipulation of male secondary sex characters on female mate preference in red jungle fowl. *Anim. Behav.* 44:999–1006.
- Zuk, M., R. Thornhill, J. D. Ligon, and K. Johnson. 1990a. Parasites and mate choice in red jungle fowl. *Am. Zool.* 30:235–244.

Zuk, M., R. Thornhill, J. D. Ligon, K. Johnson, S. Austad, S. H. Ligon, N. W. Thornhill, and C. Costin. 1990b. The Role of Male Ornaments and Courtship Behavior in Female Mate Choice of Red Jungle Fowl. *Am. Nat.* 136:459–473.

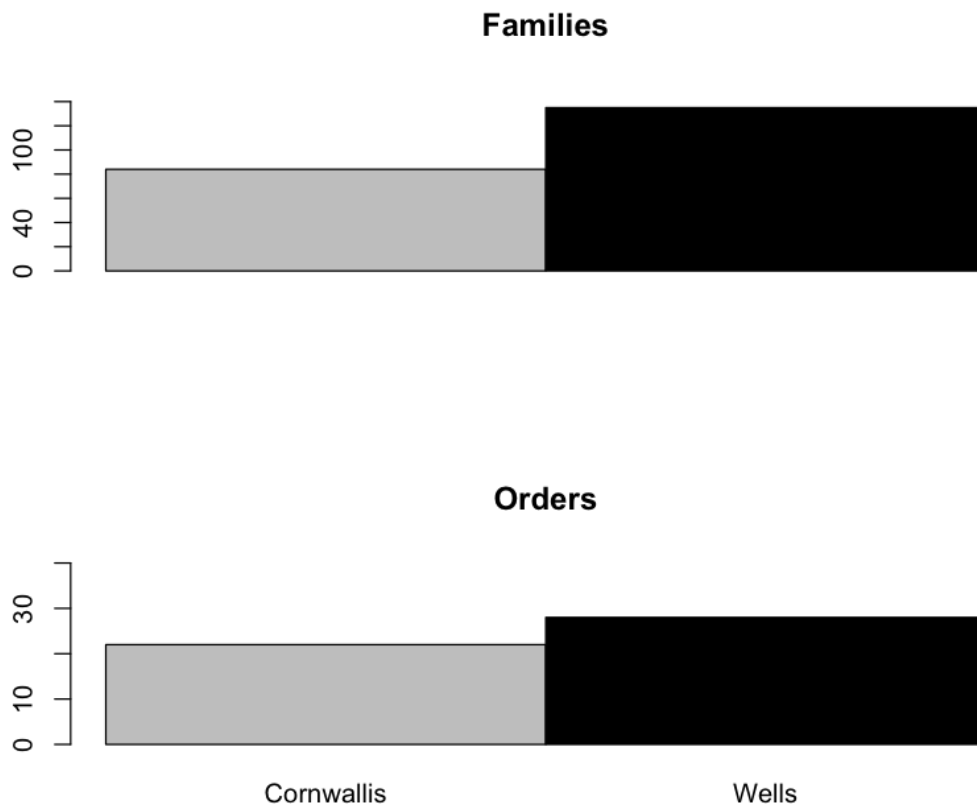
APPENDIX 1

Appendix Table 1.1 - Table of models constraining the rate of change from non-cooperative to cooperative breeding to be identical in both parasitized and non-parasitized backgrounds. If the transition differences between these two backgrounds, this model should have a *worse* fit than the dependent model.

	Likelihood	Harmonic Mean	log₁₀ K
Ericson Backbone			
Dependent Model	-3517.268 ± 0.058	-3519.124	0.965
Restricted Model	-3519.491 ± 0.061	-3522.694	—
Hackett Backbone			
Dependent Model	-3523.845 ± 0.067	-3525.65	1.533
Restricted Model	-3527.376 ± 0.061	-3528.656	—
Africa (Hackett Backbone)			
Dependent Model	-942.554 ± 0.055	-943.202	—
Restricted Model	-942.331 ± 0.07	-943.021	0.097
Africa (Ericson Backbone)			
Dependent Model	-940.038 ± 0.039	-941.489	—
Restricted Model	-939.449 ± 0.079	-941.874	0.256
Australia (Hackett Backbone)			
Dependent Model	-500.397 ± 0.096	-501.521	0.617
Restricted Model	-501.817 ± 0.11	-503.301	—
Australia (Ericson Backbone)			
Dependent Model	-497.843 ± 0.103	-499.887	0.707
Restricted Model	-499.47 ± 0.085	-500.521	—

APPENDIX 2

Appendix Figure 2.1 - Family and order differences between this study and Cornwallis. Families and orders are both increased in the Wells dataset as compared with the Cornwallis dataset.



APPENDIX 3

Appendix Table 3.1 - Hackett backbone tree top models for general linear model analysis (n=100).

Top Models Hackett Backbone										
Model	PC1	PC2	PC3	Host	Testis	PC1:PC2	PC1:PC3	PC2:PC3	PC3:Testis	% Trees Hackett
314	—	—	—	0.1011506	0.04049489	—	—	—	—	83
209	—	—	—	—	0.04414895	—	—	—	—	67
105	—	—	—	0.11056565	—	—	—	—	—	55
328	0.00672729	—	—	0.10725371	0.04264839	—	—	—	—	30
367	—	—	-0.0070061	0.10467823	0.04294107	—	—	—	—	16
223	-0.0008446	—	—	—	0.0460422	—	—	—	—	15
341	—	0.0128833	—	0.09903611	0.04279269	—	—	—	—	15
262	—	—	-0.0069503	—	0.04544043	—	—	—	—	14
236	—	0.0151828	—	—	0.04598042	—	—	—	—	10
119	0.00795662	—	—	0.11115343	—	—	—	—	—	6
772	0.00794608	-0.0046812	—	0.11466053	0.04524635	-0.0259236	—	—	—	6
132	—	0.01210942	—	0.10239015	—	—	—	—	—	5
158	—	—	0.00025359	0.12356347	—	—	—	—	—	5
667	-0.0011879	-0.0029726	—	—	0.04690499	-0.0254787	—	—	—	4
27	—	0.02168797	—	—	—	—	—	—	—	4
563	0.00443052	-0.0077529	—	0.11775112	—	-0.02591	—	—	—	3
13575	—	—	0.00714283	—	0.04289101	—	—	—	-0.0341498	3
53	—	—	-0.0170677	—	—	—	—	—	—	2
276	0.00743023	—	-0.0127334	—	0.05232006	—	—	—	—	2
1954	—	—	-0.0211445	—	0.05532275	—	—	0.06077407	—	2
14	-0.0005668	—	—	—	—	—	—	—	—	1
250	0.01244488	0.00830534	—	—	0.04842083	—	—	—	—	1
289	—	0.02457201	-0.018108	—	0.05403421	—	—	—	—	1
355	0.0113533	0.01583239	—	0.12491398	0.04276464	—	—	—	—	1
458	0.00013264	-0.0025601	—	—	—	-0.0251964	—	—	—	1
2059	—	0.02511285	-0.0432273	0.06374454	0.05187519	—	—	0.04901791	—	1
2385	-0.0025437	0.00210635	-0.0167621	—	0.0581992	-0.0267675	—	0.05410313	—	1
13680	—	—	0.01479837	0.09194944	0.03987947	—	—	—	-0.0339745	1
15372	—	0.01509605	-0.019809	0.08701789	0.04797919	—	—	0.05852652	-0.0117477	1

Appendix Table 3.2 - Ericson backbone top models for general linear model analysis

(n=100).

Model	PC1	PC2	PC3	Host	Testis	PC1:PC2	PC1:PC3	PC2:PC3	PC2:Testis	PC3:Host	PC3:Testis	% Trees Ericson
314				0.104116702	0.040127338							76
209					0.042858342							66
105				0.110891895								57
328				0.116839775	0.03976661							30
341	0.007431739			0.103064962	0.0324197							18
367				0.111869551	0.04688494							16
262			-0.007711181		0.0405943							15
236		0.007660894	-0.0044119176		0.043301425							14
132		-0.001737999		0.109015127								12
158				0.108007784								9
119	0.00697714			0.123105178								7
223	0.002554885				0.041749923							7
27												5
667	0.001903168	0.002385667			0.037580308	-0.022883082						4
772	0.008531229	-0.013390944		0.108970955	0.042122942	-0.021597204						4
53			0.010056325									3
458	-0.000594449	-0.007715985			-0.022934969							3
2059		0.013559258	-0.029725741	0.096924284	0.044474954			0.061051541				3
13575		0.01585701	0.030681119	0.103880145	0.038144381						-0.031699874	3
13680			0.020156747		0.036432502						-0.031415976	3
14												2
355	0.004318438	0.011819199		0.110458235	0.047210654							2
563	0.006471047	-0.018901205		0.064565564		-0.026088064						2
1954	0.001756691	0.025744414			0.047807921			0.066736483				2
41	0.009214476	0.006045192										1
250	0.001442252	0.024201009			0.046757206							1
276	0.010636765	-0.014660432	0.024517432		0.039716147							1
289		-0.018328328	-0.021603983	0.092160309	0.036852629							1
394			-0.021603983		0.037278488							1
900	0.008122032		-0.022862069									1
1745		0.01420298	-0.030645222									1
1968	0.000945334	0.027743857			0.052577723							1
3565		-0.024092965			0.037589097							1
6815			-0.04108219	0.124253151					0.018864752			1
7024			-0.039660434	0.116141067						0.043958046		1
14033	0.005611535	-0.014356024	0.027901391		0.035630525					0.047181634		1
20337			-0.036571139	0.0976785	0.044908687	-0.024532494				0.084167268	-0.033400045	1
											-0.034352352	1

**Appendix Table 3.4 - Australian top models for both Hackett and Ericson
backbones (n=10 trees each).**

Hackett top models									
Model	PC1	PC2	PC3	Host	Testis	PC1:PC3	PC2:Testis	% Trees	Hackett
209	—	—	—	—	0.15426402	—	—	—	100
236	—	0.042944776	—	—	0.151338938	—	—	—	80
314	—	—	—	0.157177961	0.150491472	—	—	—	60
223	-0.029998887	—	—	—	0.153085628	—	—	—	50
105	—	—	—	0.208807639	—	—	—	—	40
27	—	0.073341963	—	—	—	—	—	—	30
262	—	—	-0.023276212	—	0.153988218	—	—	—	20
900	-0.078145536	—	-0.112682528	—	—	-0.111664684	—	—	20
14	-0.025964391	NA	NA	NA	NA	NA	NA	NA	10
1109	-0.069816832	NA	-0.1487073	NA	0.160467866	-0.111695708	NA	NA	10
3565	NA	-0.026416112	NA	NA	0.144713439	NA	0.05435474	—	10

Ericson top models									
Model	PC1	PC2	PC3	Host	Testis	PC1:PC3	PC2:Testis	% Trees	Ericson
209	—	—	—	—	0.151829222	—	—	—	100
314	—	—	—	0.158602777	0.144200347	—	—	—	40
105	—	—	—	0.190621746	—	—	—	—	30
236	—	0.04260937	—	—	0.140621276	—	—	—	30
900	-0.073817077	—	-0.105512242	—	—	-0.109329556	—	—	30
1109	-0.057197559	—	-0.127676374	—	0.14015896	-0.100827395	—	—	30
27	—	0.066849241	—	—	—	—	—	—	20
223	-0.025222995	—	—	—	0.153131015	—	—	—	20
14	-0.036983689	NA	NA	NA	NA	NA	NA	NA	10

Appendix Table 3.5 - African top models for both Hackett and Ericson backbones

(n=10 trees each).

Hackett top models								
Model	PC1	PC2	PC3	Host	Testis	PC1:PC2	PC3:Host	%Hackett
105	—	—	—	0.17857026	—	—	—	100
132	—	0.00888324	—	0.16206107	—	—	—	30
27	—	0.00328131	—	—	—	—	—	20
158	—	—	-0.0052385	0.19022418	—	—	—	20
6815	—	—	-0.1065958	0.27718982	—	—	0.19784426	20
14	-0.0460042	—	—	—	—	—	—	10
53	—	—	-0.0683198	—	—	—	—	10
119	-0.0258937	—	—	0.10931977	—	—	—	10
209	—	—	—	—	0.03844527	—	—	10
314	—	—	—	0.1176639	0.01679262	—	—	10

Ericson Top models								
Model	PC1	PC2	PC3	Host	Testis	PC1:PC2	PC3:Host	% Ericson
105	—	—	—	0.17727684	—	—	—	100
132	—	-0.0202562	—	0.17327544	—	—	—	50
158	—	—	0.03846638	0.18438265	—	—	—	40
119	0.01145223	—	—	0.19562875	—	—	—	30
6815	—	—	-0.0917566	0.29924812	—	—	0.23128698	20
14	-0.0165976	—	—	—	—	—	—	10
314	—	—	—	0.2033151	-0.0450955	—	—	10
6829	-0.0009699	—	-0.1233372	0.29847169	—	—	0.27106513	10

Appendix Table 3.6 - Nearctic top models for both Hackett and Ericson backbones

(n=10 trees each).

Hackett top models								
Model	PC1	PC2	PC3	HOST	Testis	PC1:PC2	PC1:Testis	% Trees Hackett
14	0.17683545	—	—	—	—	—	—	100
119	0.17306789	—	—	-0.2148593	—	—	—	90
223	0.18252076	—	—	—	0.08075432	—	—	90
53	—	—	-0.1118221	—	—	—	—	60
41	0.1947784	-0.0542367	—	—	—	—	—	40
67	0.17908284	—	-0.1006572	—	—	—	—	20
105	—	—	—	-0.2449931	—	—	—	20
209	—	—	—	—	0.07384923	—	—	20
3579	0.17594751	0.23484989	—	—	0.05939138	—	-0.1743126	20
158	—	—	-0.1093166	-0.3223986	—	—	—	10
3618	—	0.29254854	-0.1619882	—	0.05322786	—	-0.1833682	10
3996	0.35893445	-0.6962451	—	—	0.04014896	-0.3226804	-0.254937	10

Ericson top models								
Model	PC1	PC2	PC3	HOST	Testis	PC1:PC2	PC1:Testis	% Trees Ericson
14	0.17918438	—	—	—	—	—	—	100
119	0.18087107	—	—	-0.229486	—	—	—	100
223	0.19066018	—	—	—	0.08067777	—	—	100
53	—	—	-0.1082038	—	—	—	—	50
41	0.19801677	-0.0542559	—	—	—	—	—	30
105	—	—	—	-0.2165829	—	—	—	30
67	0.18607266	—	-0.0941401	—	—	—	—	20
209	—	—	—	—	0.0720292	—	—	20
262	—	—	-0.124294	—	0.07975298	—	—	10

Appendix Table 3.7 - Neotropics top models for both Hackett and Ericson

backbones (n=10 trees each).

Hackett Top Models						
Model	PC1	PC2	PC3	Host	Testis	% Trees Hackett
105	—	—	—	0.20137443	—	100
314	—	—	—	0.19963358	0.05530784	90
158	—	—	0.06438096	0.19097859	—	50
53	—	—	0.08479057	—	—	40
132	—	0.02228367	—	0.1840655	—	40
209	—	—	—	—	0.06892282	20
341	—	0.01920861	—	0.19143827	0.06355271	20
367	—	—	0.0358453	0.20222969	0.0607796	20
119	0.00385923	—	—	0.20167443	—	10
262	—	—	0.08393007	—	0.03873935	10

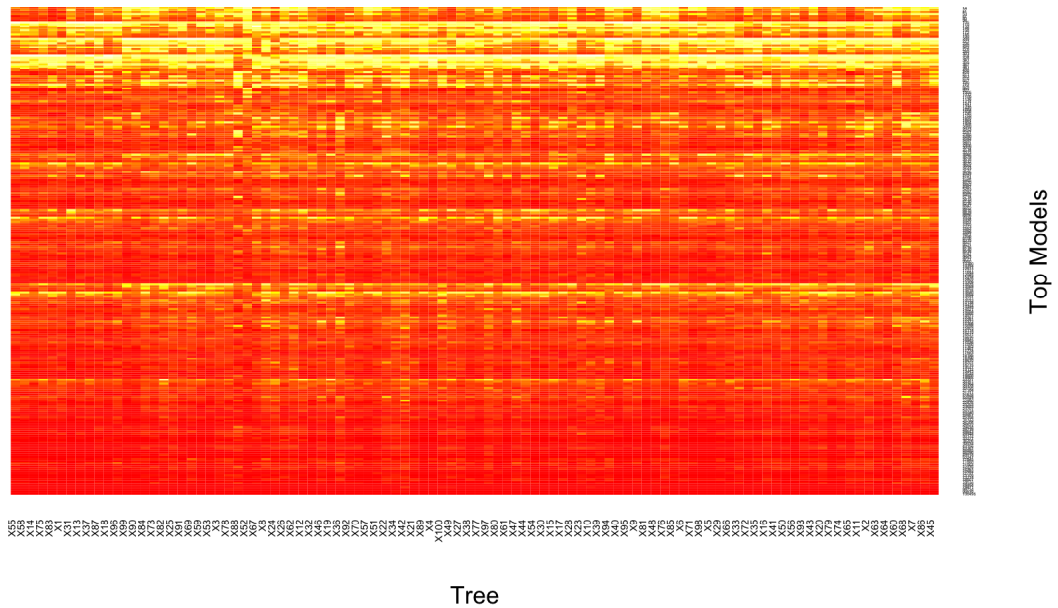
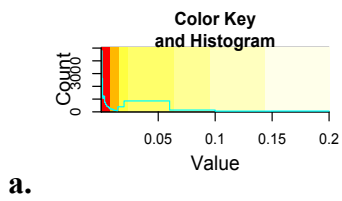
Ericson Top Models						
Model	PC1	PC2	PC3	Host	Testis	% Trees Ericson
105	—	—	—	0.19795029	—	100
314	—	—	—	0.19698812	0.05133796	70
53	—	—	0.06701478	—	—	50
158	—	—	0.05358287	0.1754293	—	50
116	0.01720227	—	—	0.21962263	—	30
209	—	—	—	—	0.05201369	20
262	—	—	0.06096746	—	0.04886588	20
367	—	—	0.04137729	0.18247922	0.05168783	20
27	—	0.03132442	—	—	—	10
132	—	0.01774022	—	0.20709799	—	10

Appendix Table 3.8 - Palearctic top models for both Hackett and Ericson backbones

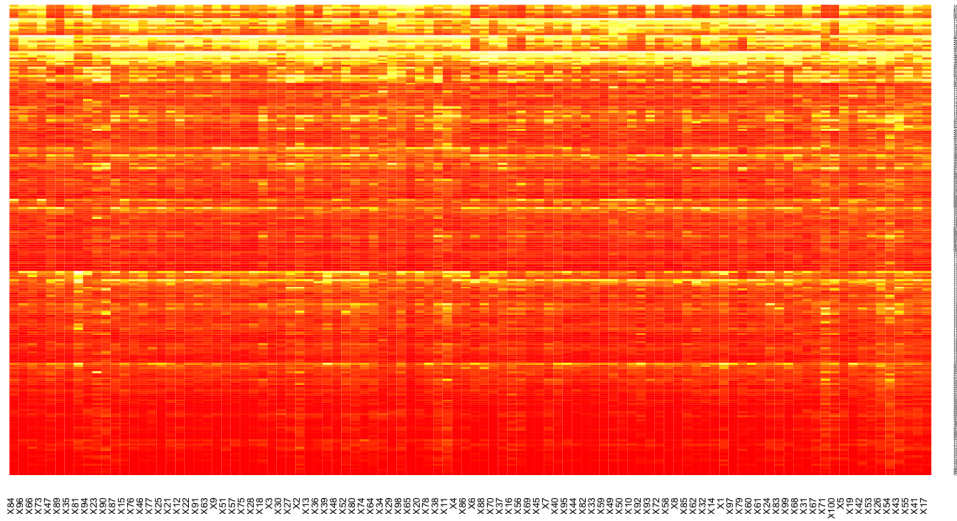
(n=10 trees each).

Hackett Top models							
Model	PC1	PC2	PC3	HOST	Testis	PC1:PC2	% Trees Hackett
27	—	-0.0505165	—	—	—	—	100
53	—	—	-0.1794739	—	—	—	100
209	—	—	—	—	0.07511477	—	100
458	0.11312997	-0.8353938	—	—	—	-0.302975	100
14	0.14044595	—	—	—	—	—	90
105	—	—	—	0.03650703	—	—	90
563	0.13571269	-1.0090426	—	0.54312805	—	-0.351363	80
Ericson Top models							
Model	PC1	PC2	PC3	HOST	Testis	PC1:PC2	% Trees Ericson
27	—	-0.0560871	—	—	—	—	100
53	—	—	-0.1826557	—	—	—	100
105	—	—	—	0.00208829	—	—	100
458	0.12388024	-0.8709228	—	—	—	-0.3170589	100
563	0.15383178	-1.0331529	—	0.54022421	—	-0.3616505	100
209	—	—	—	—	0.0695036	—	90
14	0.14439157	—	—	—	—	—	80

Appendix Figure 3.1 - Heat map for all models in all trees investigated across the (a.) Ericson and (b). Hackett backbones. Each row denotes a model. Model weights for each tree are represented the x-axis, with lighter colors indicating a greater model weight assigned to that model. Top models are the bright bands in the upper part of the map. Note the fairly uniform support for the top models, but also considerable variation across the tree and the extremely poor support for models with large parameters.



b.

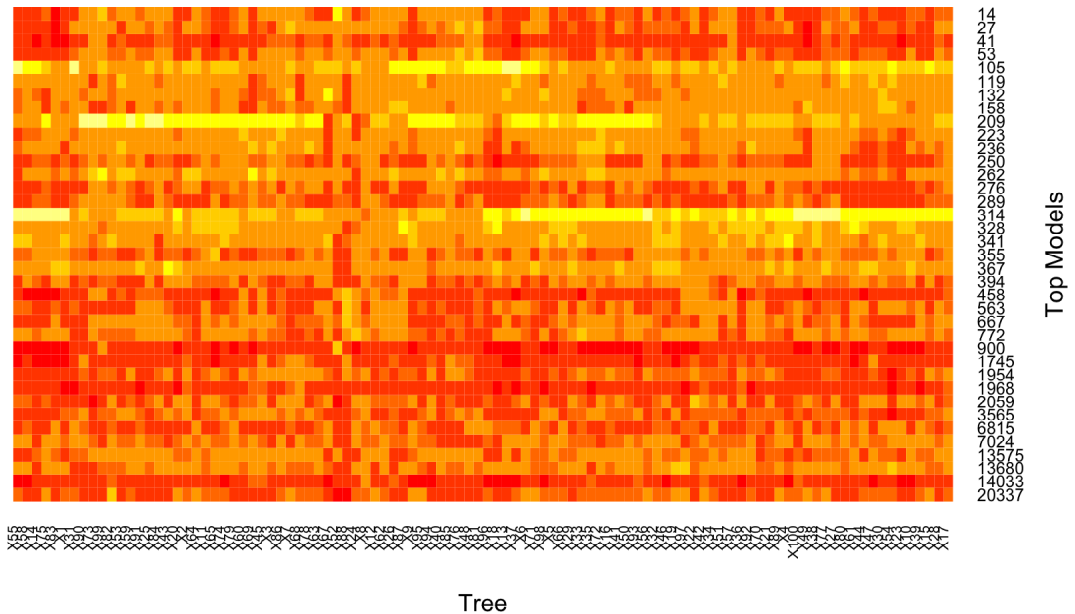


Tree

Top Models

Appendix Figure 3.2 - Heat map of the 27 top model weights across the (a.) Ericson and (b.) Hackett backbone trees. Each row denotes a model included in at least one tree as a top model ($\Delta AIC_c \leq 2$). Model weights for each tree are represented the x-axis, with lighter colors indicating a greater model weight assigned to that model. Note the three stronger bands, indicating Host, Testis, and Host+Testis, as well as the substantial differences in model weights across these and other top models between trees.

a.



b.

