Cooperative breeding in songbirds promotes female song but slows the evolution of song elaboration

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Abstract

Bird song has historically been characterized as a primarily male behavior that evolves through sexual selection pressures involved in mate attraction. More recently, researchers showed that female song is far more prevalent in songbirds than previously thought, raising new questions about how other social functions of birdsong and sexual selection pressures on females might affect song evolution. Certain breeding systems, particularly cooperative breeding, are hypothesized to change social dynamics and sexual selection pressures on males and females and may thus influence song evolution in both. Here, we construct a large-scale database synthesizing species-level information on the presence of female song, the characteristics of presumably male song, social variables, and breeding systems, and we perform comparative phylogenetic analyses. Our results suggest that cooperative breeding and female song co-occur significantly more than expected and exhibit co-evolutionary dynamics; in particular, cooperative breeding appears to decrease the likelihood that female song is lost. Notably, we find evidence that these trends might be linked to certain social features associated with cooperative breeding, including social bond stability, but not others, such as increased group size. In addition, we observe that song repertoire size appears to evolve more slowly in cooperative breeding lineages. Overall, our findings demonstrate that cooperative breeding may have complex and sex-specific effects on song evolution, maintaining female song while slowing the rate of male song elaboration, suggesting that song in cooperatively breeding species could function in ways that differ from the traditional mate-attraction paradigm and that lesser-studied functions of songs may be evolutionarily consequential.

Introduction

In *The Descent of Man and Selection in Relation to Sex*, Darwin proposed that polygyny, a mating system in which males compete to obtain multiple mates, would amplify sexual selection on male songbirds, favoring increasingly complex songs to attract females because of the potentially extreme fitness differences between attracting multiple mates and attracting none ([1], pp. 265-266). A large-scale phylogenetic analysis of male song and mating systems across the songbird lineage showed that social polygyny drives the evolution of birdsong in more nuanced ways than originally predicted by Darwin [2]: namely, polygynous mating systems increased the rate of song evolution, but not uniformly toward more complex song.

Other mating systems may change the selection pressures on females more than on males, with unknown consequences for sexually selected traits such as song. Such shifts in sexual selection pressures are thought to occur in systems that engage in cooperative breeding, a breeding system characterized by the common occurrence of alloparental care, or care by adults other than the breeding pair. Specifically, cooperative breeding has been proposed to increase sexual selection pressures on females through increased intrasexual competition for breeding status and associated increase in variance of reproductive success between individual females within a population [3,4], although the extent of this reproductive skew can vary widely by species, especially in avian taxa [5]. The effects of cooperative breeding on sexual selection pressures in males are even less straightforward. Cooperative breeding may decrease selection on males via a reduced fitness benefit from obtaining additional matings while increasing this gradient in females, an apparent reversal of Bateman's principle [6,7]. Evidence showing increased versus decreased sexual selection pressures in the context of cooperative breeding in birds has been mixed; while cooperative breeding was found to be associated with reduced sexual dimorphism in plumage coloration and body size in one songbird family [3], possibly indicating more balanced sexual selection pressures between males and females, but high plumage dimorphism in other cooperatively breeding songbird species suggests that this trend is not universal [8].

Bird song has historically been discussed as a primarily male behavior: a sexually selected, ornamental trait that functions in a number of social interactions including mate attraction, species recognition, and territory defense [9]. However, increased recognition of female song over the past decade has made it clear that this framing may be incomplete [10,11]. Data on the biological contexts of female song are sparse for most species, but, broadly, there have been several patterns of singing behavior observed in different species, including male-female duetting, agonistic female-female interactions, and within-pair or within-group interactions [11]. These behavioral patterns correspond with various hypothesized functions of female song: mate attraction, intrasexual competition, territory and anti-predator defense, and social cohesion within groups [12,13]. Species vary widely in how similar the songs are between males and females of the species [14]. If female song primarily functions similarly to male song in mate attraction or intrasexual conflict, it may also undergo sexual selection. Alternatively, the evolution of song, an inherently social behavior, may be subject to evolutionary pressures related to social factors in addition to traditionally studied sexual selection, a phenomenon that might be especially relevant in females [15]. For example, in some species it may be possible that song serves primarily social functions and is subject to minimal sexually selective pressures, as has been shown in the closest relatives of oscine songbirds, the suboscines [16].

Cooperative breeding has evolved numerous times in the avian lineage, and its repeated evolution has been facilitated by enlarged familial groups or kin neighborhoods that provide inclusive fitness benefits of cooperation and altruism, as well as opportunities for direct fitness benefits through group membership [17,18]. For example, these groups facilitate delayed dispersal of young and a greater investment in offspring, as well as provide resistance to predation though enlarged group size regardless of kinship, increasing individuals' chances of survival [19,20]. Despite its likely origins in kin-based systems [17], cooperative breeding does not occur exclusively among related individuals, though non-kin cooperative breeding is much less common. The fitness benefits and consequences of cooperative breeding, therefore, are somewhat entwined with other forms of group living. For example, in some systems, a simple increase in the size of social groups may lead to a tradeoff across different levels of organization by increasing intragroup competition while also increasing group fitness, even without overt cooperation within the group [21]. While the effect of complex breeding systems on sexual selection pressures in males and females, as well as the functions of male and female song in social species, both remain poorly understood in songbirds, several other traits related to social network stability, including territoriality, monogamy, and long-term pair bonds, are correlated with the presence of female song in various songbird clades [14]. Further, cooperative breeding appears to broadly promote increasing communicative complexity as measured by “functional vocal repertoire size” [22], which primarily counts calls, but could potentially extend to songs that serve lesser-understood socially communicative functions.

We hypothesize that the evolution of male and female songs have been influenced by the evolution of cooperative breeding systems in the Oscine songbirds. We specifically predict that the properties of male songs have not been driven in a single direction in cooperatively breeding contexts (as might be expected as a result of increased sexual selection pressure), but rather that there may be different rates of evolution in cooperative versus non-cooperative breeding lineages as we previously observed for monogamy versus polygyny [2]. We also predict that female song may be influenced by cooperative breeding, and we attempt to disentangle two potential hypotheses regarding the mechanisms linking them. First, females might be more likely to sing in cooperatively breeding species because of song functioning to promote social cohesion and cooperation, in which case we might expect species that exhibit longer social bonds or live in social groups to be more likely to evolve female song presence. Second, female song might be promoted due to increased sexual selection pressures on females in cooperatively breeding lineages, in which case we might expect other measures of sociality to be less predictive of female song evolution than cooperative breeding itself. By comparing the relationship between female song and cooperative breeding to that of other social variables, we may gain further insight into the underlying links between these behaviors.

Here, we present a novel compiled dataset that includes cooperative breeding classification and data compiled from various sources for 4373 Oscine species that we have integrated with species-level data on female song presence or absence for 1094 species and several features of (putatively male) song complexity and performance in 360 species. We use phylogenetically informed analyses to test whether cooperative breeding has influenced the evolution of syllable repertoire, number of unique syllables per song, song repertoire, song duration, inter-song interval, or the presence of female song. We find evidence that cooperative breeding may impose pressures that maintain female song and that female song may facilitate a transition to cooperative breeding, both leading to female song being more common in extant cooperatively breeding species than in non-cooperatively breeding species. We did not, however, observe a significant association with female song for other forms of social organization such as familial living, colonial living, and larger group sizes. We further show that greater co-occurrence with female song may be specific to kin-cooperative breeding, with an opposite trend observed for non-kin cooperative breeding. We also find evidence that the rate of evolution of (putatively) male song repertoire size is reduced in both kin- and non-kin-cooperatively breeding lineages as well as in lineages with familial living but not cooperative breeding. These findings suggest that female song may be particularly important with increasing social complexity and provide clues regarding how male song and female song may evolve in different contexts.

Results

Here, we combined and reconciled data sources regarding the prevalence of cooperative breeding at the species level for 4373 Oscine species. We also compiled species-level data from Griesser et al. 2017 [17] and Griesser et al. 2023 [23] on other forms of sociality beyond the breeding pair (Supplemental Tables 1-2). We further combined and updated datasets on the presence of female song in species as well as data on species-level song features encompassing song complexity and performance metrics (Supplemental Datasets 1-2).

Assessing the association between cooperative breeding and other sociality traits

First, we aimed to test which social traits were correlated with cooperative breeding. Using the assembled species-level data as character states at the tips of a published avian phylogeny [24], we compared the evolution of cooperative breeding to that of other social variables: degree of sociality, group size, duration of social bonds, familial living, colonial living, social mating system (monogamy vs. polygyny), and number of caretakers [2,17,23]. When we estimated the ancestral character histories of these variables, we found that several social variables occurred together with cooperative breeding more often than would be expected given their respective distributions across the studied species: living in a social pair or group, living in a group larger than a pair or smaller than 30 individuals, having social bonds longer than one breeding season, living with family members, *not* living in a colony, being socially monogamous, and having more than two caretakers (Table 1).

			Degree of association between states of Trait A (non-cooperative breeding versus cooperative breeding) and Trait B			
Social Trait (Trait B)	Number of species	Empirical p-value	Non-cooperative breeding co-occurrence with Social Trait = 0	Cooperative breeding co-occurrence with Social Trait = 0	Non-cooperative breeding co-occurrence with Social Trait = 1	Cooperative breeding co-occurrence with Social Trait = 1
Asocial (0) vs. social groups (1)	441	0.006	0.78	0.104	0.01	1
Asocial or pair (0) vs larger groups (1)	441	0.006	0.914	0.088	0.004	1
Asocial, pair, or small group (0) vs. large group (1)	441	<0.002	0.016	1	0.664	0.314
Social bonds lasting one season or less (0) vs longer than one breeding season (1)	472	<0.002	0.018	0.002	0.56	1
Non-familial (0) vs. familial living (1)	1159	<0.002	0.372	0.024	0	1
Non-colonial (0) vs. colonial living (1)	472	0.036	0.042	1	0.624	0.584
Monogamy (0) vs. polygyny (1)	709	0.024	0.03	1	0.62	0.49
One or two caretakers (0) vs. more than two caretakers (1)	472	<0.002	0.094	0	0	1

Table 1: Results of overlapping simulated ancestral character histories for binary social variables with those of cooperative breeding. For each pair of traits, we ran 500 ancestral character mapping simulations with the real data and 500 with shuffled data (i.e. with tip states in a randomized order) for comparison. We used methods adapted from Huelsenbeck et al. [25] to estimate an empirical *p*-value (yellow indicates significance at $p < 0.05$). Degree of association between states: Across the pairs of stochastic character maps generated from the real social trait and cooperative breeding data, we found the median proportion of the phylogeny that each combination of traits occupied, then found the fraction of randomized stochastic character map pairs that had a proportion of the tree occupying a given trait combination below the median of the real simulations. Cells highlighted in blue indicate that, in <5% of the randomized-data simulations, the fraction of the tree occupying the indicated state combination was less than the median of simulations based on real data (and thus the state combination is less common than expected if traits were evolving independently). Cells highlighted in red indicate that, in >95% of randomized-data simulations, the state combination occupied a fraction of the tree less than the median of the real simulations (thus the trait combination is more common than expected if traits were evolving independently).

Song feature evolution in the context of cooperative breeding and other sociality characteristics

We found that none of the species-level features of putatively male songs were significantly different between non-cooperatively and cooperatively breeding species when controlling for shared ancestral history (phylANOVA $p > 0.05$, Supplemental Table 3). We did, however, find that the rates of evolution of two song metrics associated with song complexity, syllable repertoire size and song repertoire size, may have differed between non-cooperative and cooperative lineages, with both evolving more rapidly in non-cooperative lineages in over 95% of simulations, though this was only significant for song repertoire size (Brownie likelihood-ratio test: song repertoire $p = 0.024$, syllable repertoire $p = 0.136$; Figure 1, Supplemental Table 4). We obtained qualitatively similar results for song repertoire evolution when we perturbed the simulations in multiple ways: using alternate criteria for reconciling differing source classifications of cooperative breeding, using cooperative breeding datasets from individual sources, using minimum or maximum reported values of species song repertoires, using species subsets obtained by jackknifing families, or using alternative methods of reconciling phylogenetic uncertainty (Supplemental Tables 4-5, Supplemental Figure 1).

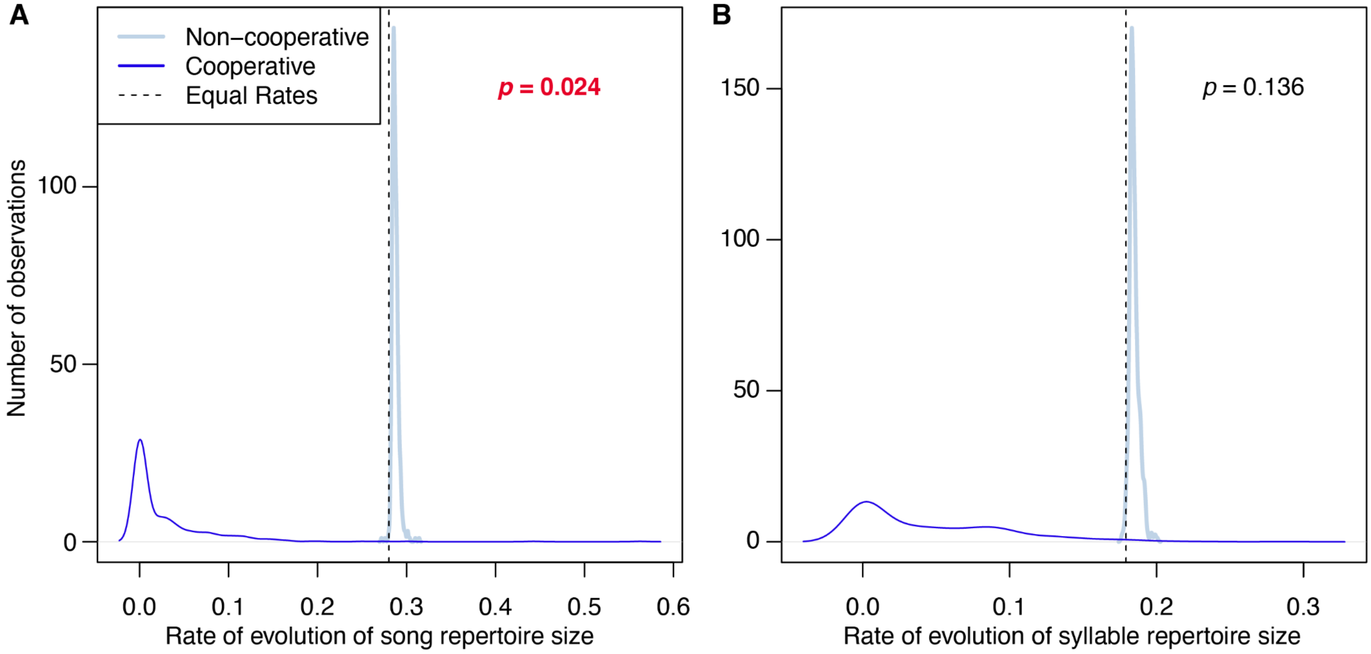

Figure 1: Testing whether the rate of evolution of (A) song repertoire and (B) syllable repertoire (both natural-log-transformed) differs based on cooperative breeding. Song repertoire evolved faster in non-cooperatively breeding lineages in 99.2% of simulations, with a Brownie likelihood-ratio test $p = 0.024$. Syllable repertoire showed a trend of faster evolution in non-cooperatively breeding lineages in 98.8% of simulations of the Brownie algorithm [26] (Brownie likelihood-ratio test $p = 0.136$). Both analyses were run for 500 simulations.

We followed up on these findings by testing whether song repertoire size was correlated with any other social traits and similarly found no significant differences in song repertoire size between species in different states of any of the discrete sociality traits (phylANOVA $p > 0.05$, Supplemental Table 3). We also tested whether song repertoire size evolved at different rates depending on the states of the various social traits. We found that song repertoire likely evolved at different rates in lineages with familial versus non-familial living (Brownie likelihood-ratio test $p = 0.0042$, faster rate of evolution in non-familial lineages in 99.8% of simulations) and with different durations of social bonds (Brownie likelihood-ratio test $p = 0.0079$, faster rate of evolution in lineages with social bonds lasting one breeding season or less in 100% of simulations) (Supplemental Table 4). We clarified the results of these evolutionary rate analyses by repeating them using the multi-state trait categorizations for group size and kin-cooperative breeding from [23] and [17], respectively. The four-state analysis of group size (asocial, pair, small groups, large groups) showed strong evidence that the rate of evolution of song repertoire is fastest in lineages whose social groups are limited in size to breeding pairs (Brownie likelihood-ratio test $p < 0.001$; Supplemental Figure 2, Supplemental Table 6). In Griesser et al. [17], social-system data for 1203 species were classified into either three or four states (see Supplemental Figure 3); our analyses showed that song repertoire evolved more rapidly in in non-familial, non-cooperative lineages than in lineages with familial living plus cooperative breeding, familial living without cooperative breeding, or non-familial living plus cooperative breeding (Brownie likelihood-ratio test: three-state $p = 0.002$, four-state $p = 0.001$; Supplemental Figure 3, Supplemental Table 7), recapitulating our findings from analyzing the two traits separately, namely that song repertoire evolves more slowly both in familial lineages and in cooperative lineages (Supplemental Table 4).

Female song and cooperative breeding

We were able to obtain species-level classifications of female song presence or absence for 1094 Oscine species, 1041 of which also had a cooperative breeding classification (Figure 2). Using the statistical method described in Huelsenbeck et al. [25], we found evidence to reject the null hypothesis that female song and cooperative breeding evolved independently (empirical $p = 0.002$), a finding primarily driven by a significantly higher-than-expected co-occurrence of female song presence and cooperative breeding (Figure 3A, Table 2). This trend in ancestral state association was not affected when the test was repeated using subsets of species created by iteratively removing individual families, showing that this trend is not driven by one particular family (Supplemental Table 8), nor when performed using a set of randomly sampled phylogenies or the consensus phylogeny calculated using an alternate method (Supplemental Figure 4, Supplemental Table 9). Despite the high degree of co-occurrence between familial living and cooperative breeding, the co-occurrence between familial living and female song was not higher than expected by chance ($p = 0.092$, Figure 3B, Table 2).

Performing a similar analysis on a smaller dataset with a more granular classification of those feature states showed that female song occurs significantly more often in systems with both familial living and cooperative breeding than expected by chance and significantly less often in systems with non-kin-cooperative and non-familial, non-cooperative systems, with an additional non-significant trend towards lower co-occurrence with familial living without cooperative breeding (Figure 3C, Supplemental Tables 10 & 11). Thus, it seems that female song may be promoted specifically when cooperatively breeding groups are made up of kin but not when familial groups live together without cooperatively breeding.

By simulating transitions between states on the same topology for breeding system and female song, we can tease out some potential directionality underlying these relationships. We found that transitions from presence to absence of female song were less frequent in cooperative breeding lineages than expected, suggesting a protective effect of cooperative breeding against loss of female song (Figure 4). Further, losing female song appears to be more likely to occur in non-cooperatively breeding lineages than expected. These trends were consistent when we ran this analysis using a set of randomly sampled trees, using the consensus tree generated using the alternate method, or using alternative classification methods for cooperative breeding (Supplemental Figure 5). Additionally, the presence of female song may promote the transition from non-cooperative to cooperative breeding, though this trend was not as robust to alternative cooperative breeding classification methods (Supplemental Figure 5C-G).

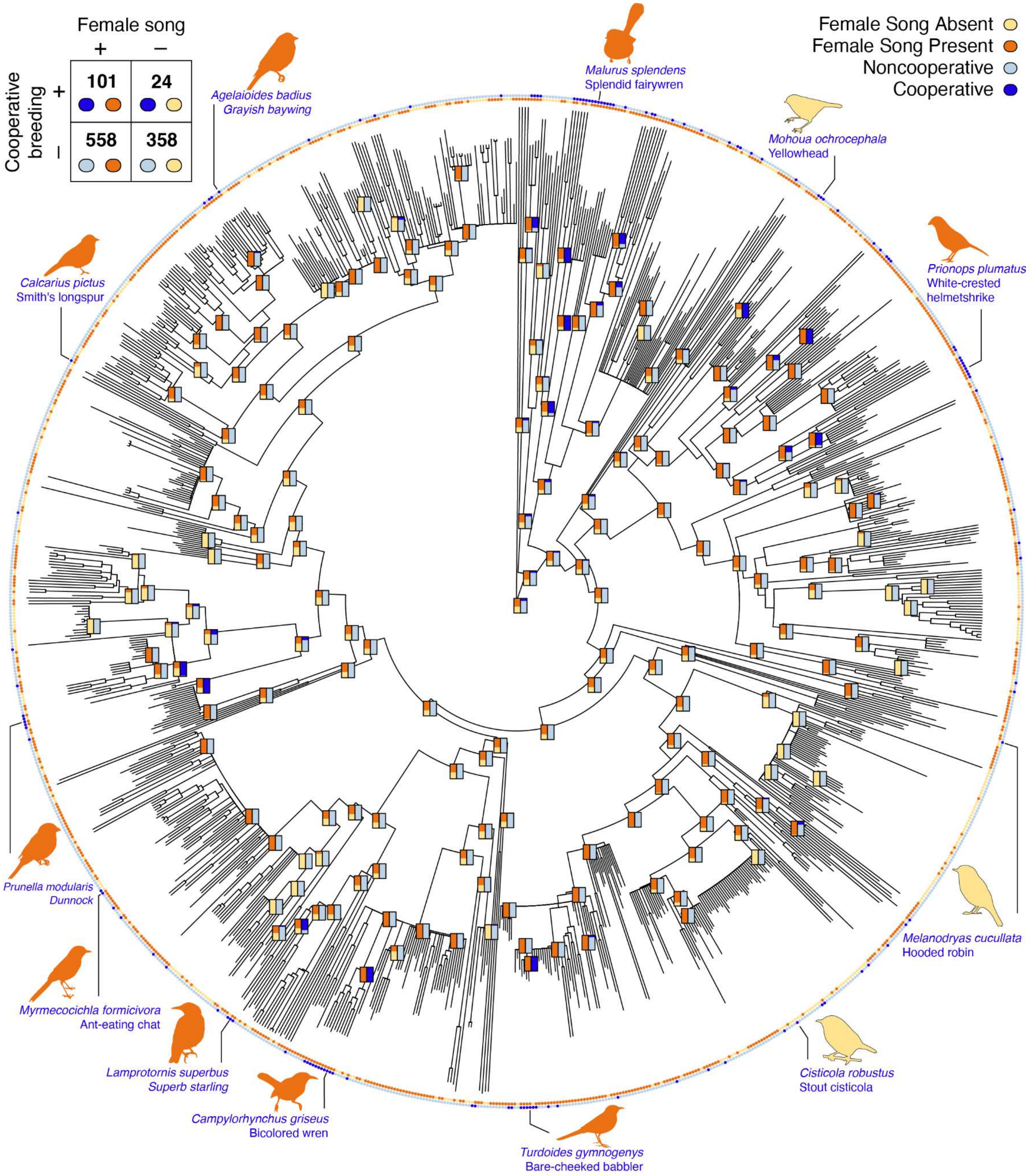

Figure 2: Phylogeny showing the classifications of cooperative breeding (outer circle) and female song (inner circle) for 1041 Oscine species. The table in the top left corner shows the number of species in each category, with female song overrepresented in cooperative breeding species. As landmarks, we illustrate several well-studied species that breed cooperatively, with their silhouettes colored according to whether female song is present in the species.

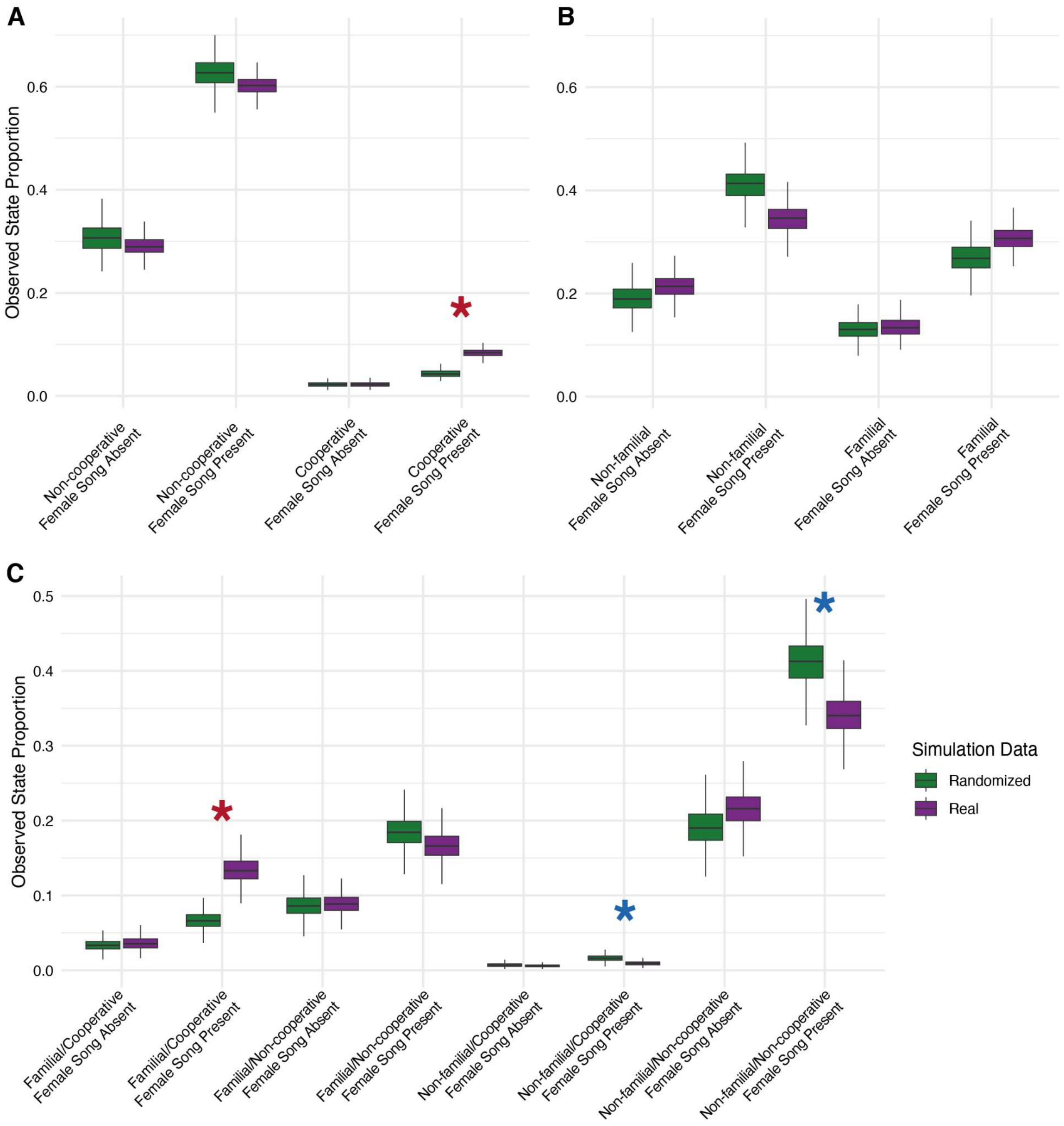

Figure 3: Overlap of stochastic character map simulations of female song and categorical social traits, measured as the proportion of the tree occupied by each state combination: A) cooperative breeding and female song (empirical *p*-value 0.002, N = 500 simulations), B) familial living (based on data from [17] and female song (empirical *p*-value 0.092, N = 500 simulations), and C) social system classification, encompassing both cooperative breeding and familial living [17], and female song (empirical *p*-value 0.0173, N = 1500 simulations). Results of post-hoc analyses comparing real and randomized simulations are shown in panels A and C; a red asterisk indicates that at least 95% of the values from the randomized simulations were less than the median value of the simulations of ancestral history based on the true data, while a blue asterisk indicates that at least 95% of the randomized simulation values were higher than the median value of the simulations of ancestral history based on the true data (see Table 2, Supplemental Table 11).

Female song and sociality

To better understand the features of cooperative breeding that might contribute to its association with female song, we repeated these analyses with species data on other social traits related to group size, social mating system, colonial living, familial living, and social bond duration (Supplemental Table 2). We found that no other traits significantly co-occurred with female song, though there were trends suggesting that female song might be more common than expected by chance in lineages with familial living (as discussed earlier, Figure 3B) and in lineages with social bonds lasting longer than a year (Table 2). A further non-significant trend suggests that female song might co-occur slightly more often than expected with small group sizes, and slightly less often than expected with pair-based social groups (Supplemental Figure 6, Supplemental Table 11). Cooperative breeding remained the only trait that significantly co-occurred with female song, but the trends in other traits could help clarify which social aspects of cooperative breeding might work together to foster female song.

Several traits, though they did not seem to co-occur with female song in the previous analyses, nevertheless appeared to evolve non-independently with female song by affecting its likelihood of being lost or gained. We found that loss of female song was more likely to occur than expected in lineages with the largest social group sizes and that female song alongside a smaller group size is a relatively stable combination, with fewer transitions out of the state than expected (Figure 5A, Supplemental Figure 7A). Conversely, we found that long social bonds, i.e. those lasting longer than one breeding season, tended to promote transition to and maintenance of female song, while shorter social bonds tended to facilitate the loss of female song (Figure 5B, Supplemental Figure 7B). This is consistent with the trends we observed for breeding system, considering that longer social bonds also tended to co-occur with cooperative breeding (Table 1). Familial living, which is associated with both cooperative breeding and longer social bonds, has a different pattern. We found that familial living tended to reduce the likelihood of either gaining or losing female song, while those likelihoods are increased in lineages with non-familial living. However, familial living is less likely to be lost when female song is present (Figure 5C). Using the subset of species with data on number of caretakers from Griesser et al. [23] reinforced our finding that lineages that had helpers at the nest, i.e. more than two caretakers, were less likely to lose female song, and those lineages without female song were less likely to increase the typical number of caretakers (Figure 5D). Intriguingly, the presence of female song appeared to greatly reduce the likelihood that a lineage would transition to fewer than two caretakers, whereas the absence of female song promoted the loss of biparental care (Supplemental Figure 7C). There were not consistent evolutionary transition-rate trends between female song and colonial living or social polygyny (Supplemental Figures 7D, E), although there is an interesting, albeit weak, trend suggesting that social monogamy with female song present as well as social polygyny without female song are both attractor states, and that transitions into those states occur more frequently whereas transitions out of those states appear to occur less frequently.

			Degree of association between Trait A (female song absent versus female song present) and Trait B			
Social Trait (Trait B)	Number of species	Empirical p-value	Female song absent co-occurrence with Social Trait = 0	Female song present co-occurrence with Social Trait = 0	Female song absent co-occurrence with Social Trait = 1	Female song present co-occurrence with Social Trait = 1
Asocial (0) vs. social groups (1)	255	0.438	0.432	0.36	0.548	0.608
Asocial or pair (0) vs larger group (1)	255	0.288	0.658	0.454	0.442	0.528
Asocial, pair, or small group (0) vs. large group (1)	255	0.316	0.392	0.464	0.772	0.494
Social bonds lasting one season or less (0) vs longer than one breeding season (1)	270	0.126	0.522	0.012	0.552	1
Non-familial (0) vs. familial living (1)	468	0.092	0.82	0.028	0.568	0.908
Non-colonial (0) vs. colonial living (1)	270	0.374	0.596	0.294	0.552	0.684
Monogamy (0) vs. polygyny (1)	323	0.248	0.128	0.716	0.758	0.62
One or two caretakers (0) vs. more than two caretakers (1)	270	0.156	0.586	0.214	0.398	0.968
Non-cooperative (0) vs. cooperative breeding (1)	1041	0.002	0.274	0.194	0.504	1

Table 2: Results of overlapping simulations of ancestral character history for binary social variables and female song. For each pair of traits (female song + a social variable from the left column), we ran 500 ancestral character mapping simulations with the real data and 500 with shuffled data (i.e. with tip states in a randomized order) for comparison. We used methods adapted from [25] to estimate an empirical *p*-value (yellow indicates significance at $p < 0.05$). Across the Trait A-Trait B stochastic character map pairs based on the real data, we found the median proportion of the phylogeny that each combination of traits occupied, then approximated the degree of association between trait states by calculating the fraction of randomized stochastic character map pairs that had a proportion of the tree occupying a given trait combination below the median of the real simulations. Cells highlighted in blue indicate that that trait combination was less than the median of real simulations in <5% of randomized simulations (and thus the trait combination is less common than expected if traits were independent). Cells highlighted in red indicate that >95% of randomized simulations were less than the median of the real simulations (thus the trait combination is more common than expected if traits were independent).

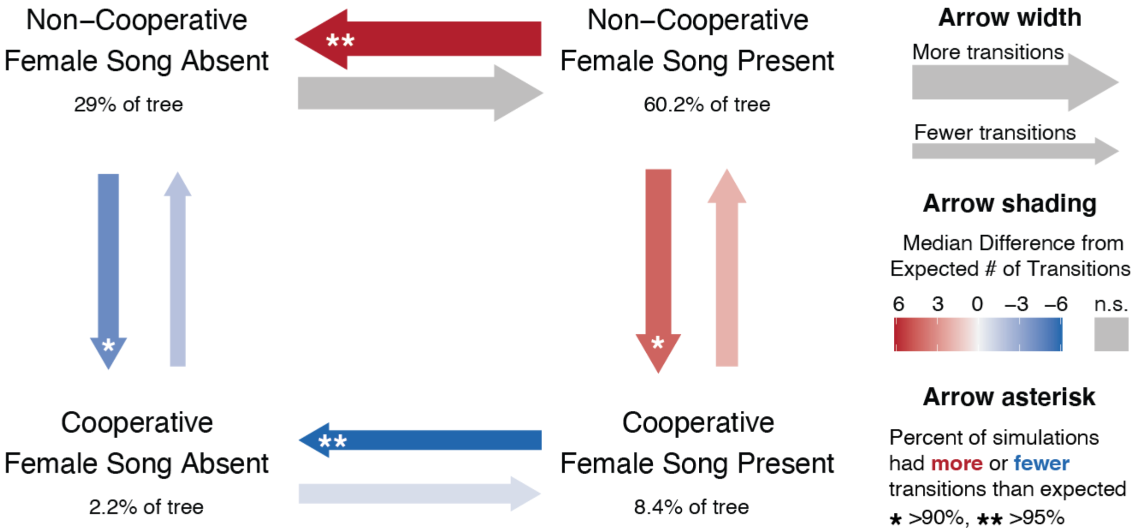

Figure 4: Female song and cooperative breeding transition likelihoods based on the median difference from expected transition counts from 500 simulations using the real trait distribution on the phylogeny. Arrow weights indicate the log-transformed median relative number of state switches that occurred on that topography. Gray arrows indicate rates for which the observed number of transitions were not significantly different from expected based on an ANOVA. Otherwise, color denotes the median difference from the expected number of transitions across simulations, with red indicating that the observed number of state switches was greater than expected, and blue indicating fewer state switches than expected. Asterisks indicate that in 90-95% (*) or >95% (**) of simulations, the number of transitions was greater (red arrows) or less (blue arrows) than the calculated expected number of transitions for the simulation in question. The percent listed under each pair of states is the median percent of the tree that is in that state-combination across all simulations.

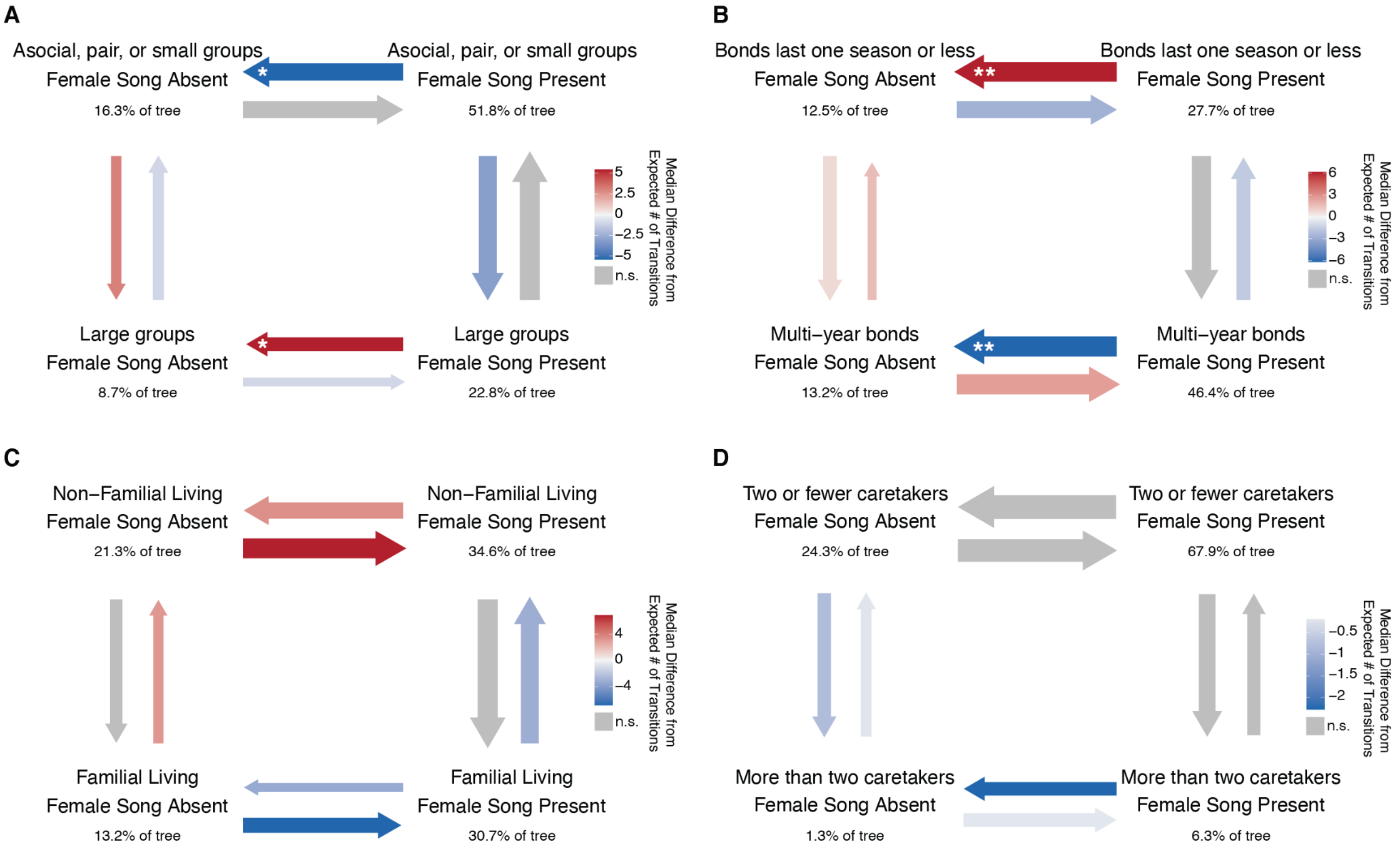

Figure 5: Transition likelihoods between female song and other forms of sociality based on the median difference from expected transition counts from 500 simulations per trait pair. Color and arrow weights vary as in Figure 4. Asterisks indicate that in in >95% of simulations (**) or 90-95% of simulations (*), the number of transitions is greater (red arrows) or less (blue arrows) than the expected number of transitions calculated for the simulation in question.

Discussion

With a set of phylogenetic comparative analyses across the songbird lineage, we find that cooperative breeding appears to co-occur with female song more often than would be expected by chance, suggesting that female song could be advantageous, and thus more likely to be retained, in this social system, as well as that female song could increase the likelihood that a non-cooperative species transitions to cooperative breeding. These findings are particularly notable given that other social variables that tend to co-occur with cooperative breeding, such as familial living, non-colonial living, social monogamy, and long social bonds, do not exhibit a significant association with female song, which we might have expected if female song was influenced broadly by increased social complexity, rather than by cooperative breeding specifically. In light of this finding, we discuss potential hypotheses about the adaptive significance of female song within cooperative breeding contexts: that female song might be more likely in species with greater social cohesion, particularly those with longer pair bonds or living in social groups, and that female song could be promoted if sexual selection pressures increase in females relative to males.

Though song is usually studied in the specific context of sexual selection through intrasexual competition and mate attraction, it is an inherently social trait that could have additional fitness effects in group-level interactions. Female song has been previously linked to territory defense (against other females, particularly in high density living [27]), mate defense (against other females, particularly in the context of polygyny [28,29]), mate attraction (towards males [30]), and coordination of breeding activities (towards mates [31] or towards offspring post-fledging [32]). However, there is additional evidence to suggest that, at least in some species, female song may have social functions beyond the pair bond, based on observations of females singing outside of the breeding season [33]. Additional functions of female song in some species include helper defense [34], individual or group-member recognition [34,35], neighbor recognition [36], and social cohesion [37]. Song that is produced in the presence of groupmates can also have non-agonistic, non-sexual contexts. The motivations and functions of these vocalizations have been studied mainly in European starlings ("gregarious song") and zebra finches (male "undirected song") and seem to serve functions that are unrelated to sexual selection [38].

Thus, song could be a mechanism that strengthens cooperative interactions through group cohesion, bonding, and coordination in species where cooperation and altruism are key life history strategies, which could be even more important in cooperative breeding systems than in species that have pair bonds and biparental care. It is intuitive that the evolution of a trait that increases the complexity of social vocal communication (female song) could be fostered in the systems that are particularly invested in those adaptations that bolster fitness of social groups. However, simply living among kin does not inherently lead to complex social coordination such as alloparenting. Our finding that the presence of female song in a species was not significantly associated with familial living, colonial living, or group size suggests that female song is not as systematically affected simply by group living or the closeness of kin as by breeding cooperatively.

In some taxa, cooperative breeding has been thought to amplify sexual selection on females when females have to compete with one another for status, with non-breeding females assisting the dominant female [39,40]. However, this may not be the case in Oscine songbirds. An analysis of 131 Oscine songbird species that frequently exhibit cooperative breeding suggested that species with male-biased helpers or mixed-sex helpers were common, whereas none of the studied species had female-biased helpers [41]. Thus, it seems more likely that any intensified sexual selection pressure on females in cooperatively breeding songbird species would be due to a perturbed operational sex ratio as a result of (young) males helping at nests rather than attempting to mate themselves. If we compare the analyses of male song evolution that we observed here with those from a previous analysis of polygynous breeding systems [2], we find contrasting patterns: the rate of evolution of syllable and song repertoire size was faster in polygynous than monogamous lineages but was slower in cooperatively than non-cooperatively breeding lineages. In addition, in parallel with our results that cooperative breeding appears to co-occur with female song and decrease its rate of loss, we found a trend in which female song appears to be more stable in combination with monogamy than polygyny, with evolutionary transitions tending to occur toward female song in combination with monogamy and away from female song in combination with polygyny. It has been generally assumed that polygyny amplifies sexual selection pressures on males, so our finding that cooperative breeding fosters female song and leads male songs to evolve more slowly could be consistent with, but does not directly test, the hypothesis that cooperative breeding reduces sexual selection pressures on males and/or increases them on females.

Our findings on the evolution of male and female song can also be compared in a familial-living context, since male song repertoire size appears to evolve more slowly in both familial and cooperatively breeding lineages. The decreased rate of evolution of song repertoire size in kin-cooperative, non-kin-cooperative, and non-cooperative familial lineages alike suggests that both familial living and cooperative breeding may stabilize male song traits, in contrast with our finding that only kin-cooperative breeding is positively associated with female song. These contrasting results may hint at sex-specific selection pressures underlying male and female song evolution. The fitness benefits of within-group altruism are expected to be greatest in kin-cooperative systems, since helper individuals obtain indirect fitness benefits of assisting in the reproduction of kin on top of many of the same direct benefits received by all helpers, related and unrelated [41]. The singular importance of this combination of factors to female song evolution suggests that this pressure towards altruism and group cohesion might be a driving force for female song evolution, while males are more affected by other pressures common to cooperative breeding and familial living. One example of a function of song that could account for these differences might be kin recognition as a mechanism of inbreeding avoidance, which is especially important in systems with extended kin contact that occur in both cooperative breeding and familial living paradigms [42]. However, if kin recognition was a significant factor in female song evolution, we would expect to observe a stronger association between female song and non-cooperative familial-living lineages; extending from our results, future field studies could address the hypothesis that male song plays a more important role in kin recognition than female song.

Our findings regarding song repertoire evolution and other social factors may provide additional context to help with interpreting our cooperative breeding results. Song repertoire size appears to evolve more rapidly in pair-based or large-group social systems, lineages with shorter social bonds, and colonial living systems, in addition to previously identified faster evolution in polygynous mating systems [2] and previously discussed faster evolution in non-cooperative, non-familial systems. Together, these may all suggest a paradigm in which male songs evolve faster, though not directionally, in environments where there is greater competition for mates due to increased social density and less social cooperation. Alternatively, the fact that several of these social factors involve group size or density, and thus the presence of more singing adults while juveniles are learning their songs, raises the question of whether male song evolution might be influenced by the number of potential tutors in juveniles' immediate surroundings. For instance, in a non-cooperatively breeding species (starlings), songs that are learned from a single male tutor are distinguishable (both by humans and conspecifics) from songs of males that learned in a larger-group social context [43]. While tutor selection and the social contexts of learning are likely very different across different species, these findings provide some evidence that simply being exposed to additional tutors could influence song evolution.

Exposure to challenging or variable environmental conditions may provide another explanation for the link between cooperative breeding and song stability. Complex songs are hypothesized to be disproportionately affected by stressful environmental conditions during development [44], and such conditions are also theorized to contribute to the development of cooperative breeding [45] or defensive behaviors [46]. The latter theory is bolstered by findings suggesting that cooperative breeding is more common in bird species found in environments with highly variable climates such as Sub-Saharan Africa, Australia, and the tropics [47–49]. Several studies have also linked cooperative breeding with life history traits indicative of individual robustness; for instance, a longer lifespan has been correlated with a higher likelihood of evolving cooperative breeding patterns [50]. Additionally, while the duration of care during the nestling and fledgling stages is comparable between cooperative and non-cooperative breeders, the post-fledgling feeding period is longer in cooperative breeders and has been linked to higher adult survivorship rates across 92 Passerine species [51]. These trends could have implications for song evolution since developmental conditions can have significant effects on young birds; a stressful upbringing can lead to impairments in both song learning and the development of the neural song system, while extended parental provisioning appears to promote the evolution of larger brain sizes across species [23]. Extended parental care and cooperative breeding could thus facilitate the evolution of songs that are more difficult to learn or help maintain song-learning capacity in harsh or highly variable environments, potentially stabilizing the song over time. Indeed, consistent with this hypothesis, we find slower song repertoire evolution in both cooperatively breeding lineages and lineages with multi-year social bonds.

Our findings could be further clarified by separating species in which females sing simpler songs or sing less frequently than males from species in which males and females sing similar songs. We also did not differentiate between species where females sing in specific contexts, for example in duets, which could evolve differently from solo female song. Our compiled data on species-level song features is presumed to be based on male song, but given the prevalence of female song across species, it cannot be ruled out that some studies inadvertently sampled females along with males. In the longer term, it would be highly informative to have species-level characterizations of both male and female songs. Finally, it has been suggested that cooperative breeding should be considered a three-state trait, separating out species that exhibit occasional cooperative breeding from those in which it is either common or absent [52]; separating the cooperative breeding trait as such might reveal more complex trends, though statistical analyses might be underpowered after splitting an already rare trait into even smaller groups.

In conclusion, we find robust sex-specific effects of cooperative breeding on singing behavior across the songbird phylogeny. Some features of male song evolve more slowly in lineages with cooperative breeding, whereas female song is disproportionately associated with cooperative breeding, suggesting that there may be relaxed sexual selection pressures on males in cooperative lineages and amplified sexual selection on females. However, the features of male song evolution that are conserved by cooperative breeding are also affected by other forms of social organization, particularly familial living, group size, and pair bond duration, whereas the presence of female song is significantly affected only by cooperative breeding. Taken together, the links between cooperative breeding and song evolution in both males and females underscore the idea that song can have social functions beyond its canonical roles in mate choice and territory defense; further, studying the evolutionary pressures exerted by cooperative breeding on songbirds may shed light on alternative functions of songs that may include the promotion of social cohesion and cooperation.

Methods

Compiling the Database

We found previously published data on cooperative breeding using the specific search criteria “Cooperative breeding in birds” and “Songbird cooperative breeding” on Google Scholar and Web of Science, yielding 11 sources with previously compiled species information on cooperative breeding [8,17,41,47–50,52–55]. We considered cooperative breeding behavior to be alloparenting during incubation, brooding, and nest provisioning in 10% or more of nests in a study, if quantitative data were available, following the classification methods of Cockburn [54]. We did not consider nest building, territory defense, or fledgling provisioning by extrapair individuals to be sufficient for cooperative breeding classification. When a source’s data were qualitative, species described unambiguously as “cooperative,” “breed cooperatively,” “often cooperative,” “facultatively cooperative breeding,” or as commonly having “helpers” at the nest were considered to be “cooperative”, and species described with “(cooperative breeding) does not occur,” “none,” “extremely rare” were considered to be “noncooperative.” We did not consider “Not observed,” “Not known to occur,” or “Never reported” to be sufficient evidence for the absence of cooperative breeding. We further did not assign a binary source classification to species if a source described it as having “occasional,” “possible,” “suspected,” “inferred,” “sometimes,” or “infrequent” cooperative breeding [52]. Cooperative breeding classifications were assigned to each species using a binary system based on the aggregation of classifications from unique sources describing the species as cooperative or non-cooperative; when one source cited another source included in our dataset we did not consider the citing source to be unique. Species for which source classifications were not unanimous were, when possible, classified based on the description in Birds of the World, otherwise they were omitted from our primary analyses (HighConfidence_Coop). To ensure that our results were robust, we repeated any analyses that produced significant results using alternative classification methods based on whether the majority of unique sources classified a species as cooperative versus non-cooperative. For those species that were “tied” with equal numbers of sources classifying them as non-cooperative and cooperative, we ran secondary analyses with these species 1) classified as non-cooperative (MeanCoopTie2Noncoop), 2) classified as cooperative (MeanCoopTie2Coop), and 3) omitted from the dataset (MeanCoopOmitTies). We also ran analyses with 4) any species with at least one source classification of cooperative breeding designated as cooperative (AnyCoopEqualsCoop) and 5) any species with at least one source classification of non-cooperative breeding designated non-cooperative (AnyNoncoopEqualsNoncoop) (see Supplemental Table 1). We also repeated analyses using the subset of classifications from several individual sources (see Supplemental Dataset 2).

To tease apart the effects of breeding systems and broader social structures, we also obtained species classifications for several metrics of sociality from [23]. We binarized several categorical metrics from that study (Supplemental Table 1). We also included binary classifications of species as socially monogamous or socially polygynous from [2] and as having familial or non-familial living from [17]. We also included multi-state traits for social group size from Griesser et al. [23] and the interaction of familial living and cooperative breeding from Griesser et al. [17].

In addition, we combined and updated published databases on the presence of female song in songbird species in natural conditions [10,56–58], Supplemental Dataset 3), which we located by performing searches on Google Scholar and Web of Science for “Female song passerine/passeriformes” and “Female song songbird”. We considered a species to have female song if it was classified as such in one of the published female song databases or if a source unambiguously said that females sing. Whenever sources disagreed on female song classification, we first attempted to resolve these discrepancies by cross-referencing with the species entry in Birds of the World [59]. If one of the sources for female song in a species with source discrepancies included Garamszegi et al. [57], we also cross-referenced these classifications with their original source in the encyclopedia *Birds of the Western Palearctic* [60]. We also used data from [61], but since the species classifications in that source created binary variables for female solo song, absence of female song, and duetting (a category that included chorusing species, which may include species in which only males sing), we only used species classifications that indicated that females produced solo song or did not sing. We further checked Birds of the World if a species was very well studied (i.e. had at least one publication noting species song features and at least one publication regarding female mating behavior in the species) but did not appear in any female song database. Species in which females had only ever been documented singing after treatment with estradiol or testosterone were omitted from our dataset, even if another source classified them as having female song present. Documentation of subsong in females in a species was not considered sufficient for a classification of female song present.

We obtained species data on syllable repertoire (average number of syllables a bird can produce), syllables per song (average number of unique syllable a bird sings per song), song repertoire (the number of individual songs a bird knows), song duration (the length of a song), and inter-song interval (time between songs) from Snyder and Creanza [2] and added several more species-level data points to the database (Supplementary Dataset 1). Whenever we obtained data for a species whose name was not present in the BirdTree.org phylogeny, we searched Avibase for alternative taxonomic classifications. If an alternative species name was present in the BirdTree phylogeny (e.g. the genus or species name has been updated), we recorded the species data in our database under the BirdTree-matching name.

Generating Consensus Phylogeny

To analyze evolutionary patterns in light of the relationships between species, we downloaded 1000 trees randomly sampled from a pseudo-posterior distribution of trees using the Hackett backbone from BirdTree.org [24,62]. We subsetted these trees to include only the 5,966 passerine species (including Oscines and Suboscines) represented in the trees. We then used the consensus.edges function (R package: phytools, with method="mean.edge" and the default setting if.absent="zero", which treats missing edges as zero in the mean edge calculation, but see "Accounting for phylogenetic uncertainty" below for other approaches) to build a consensus tree with branch lengths that included all passerine species. For all subsequent analyses, we removed the suboscine clade and only Oscine species were included in reference phylogenies.

Statistical Analyses

We conducted various phylogenetic comparative analyses by adapting code and methods from Snyder and Creanza [2]. We conducted ancestral character estimations (function ace, R package: ape) using the maximum likelihood method to estimate the evolutionary history of discrete traits (e.g. cooperative breeding, sociality metrics, female song presence) across all Oscine species for which we had a classification for a given trait. Using a likelihood ratio test, we compared the fits of the ancestral character estimation model that assumed “Equal Rates” (ER) of transition between binary (“0” and “1”) states and the model that assumed “All Rates Different” (ARD) (Supplemental Table 12). For traits with three or more states, we also tested the model that assumed “Symmetric” (SYM) rates. In subsequent analyses, we used the ARD model whenever it was significantly better than the ER model (and SYM model, when applicable). Whenever generating models of trait evolution on subsets of species, to avoid any potential bias from recalculating rates for each species subset, we used the transition rates between states that were obtained from the full set of Oscine species that had a state classification for that trait.

Song feature evolution

To determine whether there was a difference in the values of various song characteristics between groups of species that exhibit certain social traits, e.g. cooperatively and non-cooperatively breeding species, we used a set of phylANOVA analyses (R package: phytools, [63]) to compare natural log-transformed song characteristics (obtained from [2]) between the sets of species in the different social trait categories, with 50,000 simulations per song feature + social trait comparison.[2].

We then tested whether any song characteristics evolved at different rates when in a cooperative breeding state versus a noncooperative breeding state using the Brownie algorithm [26]. We generated 500 stochastic character maps, which simulate ancestral gains and losses of cooperative breeding given the transition rates calculated above, using make.simmap (R package: phytools), and used them in the brownie.lite function (R package: phytools). We performed a follow-up Brownie analysis using each of the binarized sociality traits and song repertoire size, which was found to consistently evolve faster in noncooperative than cooperative lineages across simulations. We further performed Brownie analyses on song repertoire size evolution and the multistate traits of group size ("grouping" from [23]) and the intersection of familial living and cooperative breeding traits from [17], with transition rates obtained from ape::ace() with the All Rates Different (ARD) setting, after testing and confirming that the ARD model was significantly better than both the Equal Rates (ER) and Symmetric Rates (SYM) settings.

Analyzing Evolutionary Co-occurrence of Cooperative Breeding and Female Song

To test whether pairs of discrete traits—including cooperative breeding, other sociality classifications (Supplemental Table 1), and female song presence—co-occurred in the songbird lineage more often than expected by chance, we employed methods adapted from Huelsenbeck, Nielsen, and Bollback [25]. This process involves generating stochastic character maps (simmaps) using phytools::make.simmap() for the two discrete characters in question (for example, cooperative breeding and female song) and setting the rates of transition between states (Q) to those estimated using ape::ace(). Then, for each pair of simmaps we calculated the proportions of the branches of the phylogeny spent in each of the four state combinations arising from combinations of the two binary traits (or more than four when testing one of the multi-state traits versus female song) using phytools::map.overlap(). We then calculated the statistic D (equations given in [25]) to obtain an overall measure of the disagreement between observed and expected proportions of each combination of characters. Per [25], we repeated this process to generate simulations of the two discrete traits evolving independently from one another. To do this, we randomly shuffled the tip states at the same proportion as the actual species classification data, then generated each simmap with phytools::make.simmap(). The empirical p-value is calculated as the fraction of randomized-data simmap pairs that have a D statistic larger than the mean D statistic of the simmap pairs generated from the real data. We also tried using phytools::sim.history() to generate the simulated independent evolution simmaps using the rates of transition between noncooperative breeding and cooperative breeding and between female song absent and present obtained from make.simmap(). We found that these rate-based stochastic character maps that were simulated forward in time from the root of the tree toward the tips, rather than stochastic character maps that were simulated backward in time from the tips toward the root, resulted in very different proportions of the tree falling in each state, and that the dominant state was determined primarily by which state was randomly chosen as the ancestral state in sim.history(). Therefore, we opted to use the set of simulated-independent simmaps for each trait that were made using randomly sampled tip states and make.simmap(). Unless otherwise noted, we performed 500 real and 500 simulated-independent simulations per trait comparison.

Additionally, we used the simmaps generated using the real tip states to estimate whether the state of one trait influenced the likelihood that certain transitions occurred in the other trait. For each pair of trait simmaps, denoted here as trait A and trait B, we identified every state transition in each direction (trait $A_{0\rightarrow1}$ and trait $A_{1\rightarrow0}$) on the trait A tree, then identified which state was present at the same point on the trait B tree, and vice versa. This gave us 8 observed transition counts, “trait $A_{0\rightarrow1}$ in trait B_0”, “trait $A_{0\rightarrow1}$ in trait B_1”, “trait $A_{1\rightarrow0}$ in trait B_0”, “trait $A_{1\rightarrow0}$ in trait B_1”, etc. We calculated the expected number of transition counts for each simmap pair by multiplying the total number of trait A transitions in each direction by the fraction of the tree spent in each state of trait B, and vice versa. We performed an ANOVA on the interaction between the expected and observed rates to determine whether any differences between the observed and expected number of state-switches for each transition were significant.

Testing whether observed trends are driven by individual families

We repeated all analyses comparing song traits and cooperative breeding with significant results by performing a jackknife analysis by family, i.e. iteratively removing each family from the dataset and recalculating the results to ensure that no single family was driving the observed trends. Family classifications were obtained from AVONET [64].

Accounting for phylogenetic uncertainty

We built a second consensus tree from the same sample of 1000 trees from BirdTree.org (Hackett-Stage2, trees 3001-4000) using the consensus.edges function (R package: phytools) with method “mean.edge” but ignoring missing edges in the edge length calculations (if.absent="ignore"). To test whether this alternate method of calculating branch lengths meaningfully affected the results, we used this consensus tree to repeat tests that found significant associations between song features and cooperative breeding and between female song and cooperative breeding. To further account for phylogenetic uncertainty, we re-ran these same analyses on 200 individual trees from BirdTree.org, with 20 simulations per tree. For these, we used the transition rates calculated using the default consensus tree to generate stochastic character maps on each individual sampled tree.

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