



Territoriality, Social Bonds, and the Evolution of Communal Signaling in Birds

Joseph A. Tobias^{1,2*}, Catherine Sheard¹, Nathalie Seddon¹, Andrew Meade³,
Alison J. Cotton⁴ and Shinichi Nakagawa^{5,6}

¹ Department of Zoology, Edward Grey Institute, University of Oxford, Oxford, UK, ² Department of Life Sciences, Imperial College London, Ascot, UK, ³ School of Biological Sciences, University of Reading, Reading, UK, ⁴ Bristol Zoological Society, Bristol Zoo Gardens, Bristol, UK, ⁵ Department of Zoology, University of Otago, Dunedin, New Zealand, ⁶ Evolution and Ecology Research Centre and School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia

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*Correspondence:

Joseph A. Tobias
j.tobias@imperial.ac.uk

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Communal signaling—wherein males and females collaborate to produce joint visual or acoustic displays—is perhaps the most complex and least understood form of communication in social animals. Although many communal signals appear to mediate competitive interactions within and between coalitions of individuals, previous studies have highlighted a confusing array of social and environmental factors that may explain the evolution of these displays, and we still lack the global synthesis needed to understand why communal signals are distributed so unevenly across large taxonomic and geographic scales. Here, we use Bayesian phylogenetic models to test whether acoustic communal signals (duets and choruses) are explained by a range of life-history and environmental variables across 10328 bird species worldwide. We estimate that duets and choruses occur in 1830 (18%) species in our sample and are thus considerably more widespread than previously thought. We then show that global patterns in duetting and chorusing, including evolutionary transitions between communal signaling and solo signaling, are not explained by latitude, migration, climate, or habitat, and only weakly correlated with cooperative breeding. Instead, they are most strongly associated with year-round territoriality, typically in conjunction with stable social bonds. Our results suggest that the evolution of communal signals is associated with the coordinated defense of ecological resources by stable coalitions of males and females, and that other widely reported associations are largely by-products of this underlying trend.

Keywords: birdsong, chorusing, cooperation, duetting, ecological competition, resource defense, sociality

INTRODUCTION

Communal signals are joint visual or acoustic displays produced when two or more individuals coordinate their signaling behavior, a communication strategy widespread in social animals, including crustaceans (Tóth and Duffy, 2005), primates (Müller and Anzenberger, 2002), and birds (Hall, 2009). A key feature of these signals is that male and female animals both contribute to a combined signal, often with extreme temporal precision, as in the case of many avian duets and choruses (Mann et al., 2006; Hall and Magrath, 2007). Duetting and chorusing are perhaps not

ancestral, but nonetheless an ancient trait in birds (Logue and Hall, 2014; Odom et al., 2014), and a common feature of species in which both sexes sing (Slater and Mann, 2004). Thus, the question of why birds signal communally is central to understanding the factors driving song evolution in females and maintaining song as a trait in both sexes.

Numerous hypotheses have been proposed for the function of communal signals (Hall, 2009), generally based on the concept of competition for either ecological resources, or mates and mating opportunities (Farabaugh, 1982). Ecological hypotheses highlight the importance of cooperative defense of home ranges and foraging territories, with duets and choruses signaling the relative competitive ability of coalitions in terms of quality, stability, or numerical advantage (McComb et al., 1994; Seddon and Tobias, 2003; Radford and du Plessis, 2004; Hall and Magrath, 2007). Social hypotheses focus instead on pair or group bonds, suggesting a role for communal signals in guarding against extra-pair or extra-group fertilization (Sonnenschein and Reyner, 1983; Seddon and Tobias, 2006; Tobias and Seddon, 2009), defending positions in partnerships or groups (Rogers et al., 2007) or signaling commitment between breeding partners (Wickler, 1980). Of course, these factors are not mutually exclusive as territorial behavior and social bonding have partially overlapping functions, perhaps explaining why previous studies have found mixed support for both sets of ideas (Hall, 2000; Marshall-Ball et al., 2006; Rogers et al., 2007; Mennill and Vehrencamp, 2008).

Another obstacle to disentangling the drivers of communal signal evolution is that several alternative proximate explanations have been proposed. For example, duets and choruses are more often reported in the tropics, and thus may simply be associated with latitude, temperature, or climatic stability (Slater and Mann, 2004; Logue and Hall, 2014). Similarly, communal signals are often a feature of social and sedentary species, perhaps because they are a by-product of cooperative breeding (Seddon and Tobias, 2003; Radford and du Plessis, 2004), or otherwise associated with long-term monogamy (Benedict, 2008) and stable social bonds in general (Logue and Hall, 2014). The same pattern viewed in reverse may explain the rarity of duetting in migratory lineages, where social bonds are more likely to break down (Logue and Hall, 2014). Habitat may also play a role, particularly as pair or group members are thought to maintain contact using acoustic communal signals in habitats where visual signals are ineffective, such as dense forests (Slater, 1997; Slater and Mann, 2004; Mennill and Vehrencamp, 2008).

Many of these social and environmental factors are closely interrelated, making it difficult to interpret experimental results in single species studies (Hall, 2000; Seddon and Tobias, 2006; Rogers et al., 2007; Tobias and Seddon, 2009), and creating a severe challenge for comparative analyses (Benedict, 2008; Logue and Hall, 2014). Furthermore, previous analyses have only used incomplete sets of predictors related to key hypotheses, with poor coverage of territorial behavior and social bonds. Thus, our understanding of communal signaling remains patchy and the extent to which we can generalize from previous results is unclear (Odom et al., 2015).

We addressed these issues by compiling information on territoriality, sociality, and the occurrence of duets and choruses

across 10328 bird species (99% of extant species richness; see Appendix B in Supplementary Material). For each species, we estimated the standard duration of territory defense and social bonds, as well as the density of their primary habitat. All species were scored for migration and cooperative breeding, and we also used geographical range polygons to quantify environmental predictors, including latitude and climatic stability. These datasets offer a useful perspective on the relative roles of social and environmental factors in regulating song evolution in both sexes, particularly as the taxonomic sampling is so comprehensive.

Most studies investigating the function of communal signaling in birds have focused either on single species or single clades (e.g., Odom et al., 2015). The most extensive analyses to date have dealt with a regional passerine avifauna (300 North American species; Benedict, 2008), or subsets (<5 %) of the global avifauna with high quality data (Logue and Hall, 2014). While these studies have highlighted potential mechanisms, they are sensitive to regional or taxonomic biases in the availability or quality of data, along with other sampling effects (e.g., tropical species are absent from the North American sample). Our approach is designed to assess general patterns while minimizing sampling effects by revising and updating data from all birds, the largest terrestrial vertebrate radiation. We further account for variation in data quality by assigning all species to one of four categories of uncertainty (see Materials and Methods).

We conducted two analyses. First, we combined all intrinsic and extrinsic traits, along with the evolutionary relationships among lineages, into a Bayesian mixed model (Hadfield, 2010; Hadfield and Nakagawa, 2010). This method can be used to identify key correlations but is much less informative about the sequence of evolutionary events giving rise to duets and choruses over time. Thus, we used a second Bayesian analysis of correlated evolution (Pagel and Meade, 2006) to estimate transition rates to and from communal signaling under a range of different character states. We used these analyses to clarify the extent to which ecological, social, and environmental drivers provide the most general explanation for global patterns in communal signaling, and whether the evolution of intrinsic life history traits facilitates the evolution of communal signaling (or vice versa).

MATERIALS AND METHODS

Definitions

We define communal signaling as an acoustic display involving two or more members of a social unit, including both males and females. Their contribution to the display must include long-range acoustic signals that are coordinated or stereotyped in some way, whether they be loosely synchronous, regularly alternating, or precisely interwoven. In many cases, the primary long-range acoustic signal in birds is termed the “song,” but because we are interested in the underlying processes giving rise to communal signals, our definition extends beyond songs to include other long-range vocalizations with song-like functions, including non-vocal signals. Thus, for example, coordinated calling by pair-members in some seabirds is considered duetting (Bretagnolle, 1996), as is joint drumming by male and female

woodpeckers (*Picidae*). Our definition includes all classic duets and choruses (Farabaugh, 1982), but excludes various multi-individual vocalizations, including contact calls, alarm calls, and flight calls. Further, details on discriminating these categories are given below.

In line with convention, we defined duets as communal signals involving two individuals, whereas choruses involve three or more individuals. Following previous studies (e.g., Logue and Hall, 2014), we pooled duetting and chorusing species together in our main analyses because (1) the division between them is very imprecise with many chorusing species occasionally duetting, and vice versa, causing much confusion in the literature, and (2) both forms of behavior are likely to evolve through similar mechanisms (Seddon, 2002; Seddon and Tobias, 2003).

We also collated data on key intrinsic and extrinsic factors hypothesized to play a role in the evolution of communal signaling (Hall, 2009). Specifically, following previous studies (Jetz and Rubenstein, 2011; Salisbury et al., 2012; Pigot and Tobias, 2015), we classified species according to their degree of territoriality (non-territorial, weakly territorial, or year-round territorial); social bond stability (solitary, short-term bond, or long-term bond); type of mating system (cooperative or non-cooperative); movement (non-migratory, partially migratory, or migratory); and habitat (open, semi-open, and dense).

We defined year-round territoriality as territory defense lasting throughout the year rather than residency within a restricted area. For example, species that are vocal and aggressive (responsive to playbacks) for part of the year, and then remain in the same general area silently and unobtrusively for the rest of the year, are classified as seasonally rather than year-round territorial. We defined long-term social bonds as pair or group bonds extending beyond a single year, although this does not necessarily imply that they are year-round. Thus, migratory species in which pair members habitually reunite in subsequent breeding seasons are treated as having long-term social bonds. A detailed rationale, with explanation of our assignment of species to all these categories, is given in Appendix A of Supplementary Material, and summarized in **Table 1**.

Data Collection

We compiled data from field observations, feedback from regional experts, published literature, sound archives, and other online sources of information. Details of signaling behavior, social system, territorial behavior, and movements in birds were compiled in a global database through direct observations by JAT and NS. Observations of >4000 breeding bird species spanned a 20-year period including fieldwork in Europe, the Middle East and North Africa, sub-Saharan Africa, Madagascar, South-east Asia, Australasia and the South Pacific, and extensively in North, Central and South America, with a focus on female song, duetting behavior, social systems and year-round movements (see, e.g., Tobias and Williams, 1996; Tobias and Seddon, 2000, 2003a,b; Seddon et al., 2002, 2003; Tobias, 2003b; Tobias et al., 2008, 2011). Throughout, playbacks were routinely used to assess the strength and seasonality of territory defense, and the contribution of males and females to territorial interactions, at different seasons when possible. To augment these observations, we solicited

feedback from field biologists and ornithologists with experience of particular regions or clades. This included a number of professional birding guides who together observe >5000 bird species per annum, often using playback to show rare species to clients.

In addition to information generated from fieldwork, we conducted a thorough review of published literature and online resources. A major source of information was *The Handbook of the Birds of the World* (HBW) series (del Hoyo et al., 1992-2013), comprising 16 edited volumes of species and family accounts for all known bird species. The referenced species accounts, including sections dedicated to vocalizations and movements, are compiled by experts in focal taxa. This information was supplemented by family monographs, regional handbooks and key digital resources, such as Birds of America Online. We also conducted extensive searches for information on communal signaling through primary electronic databases (e.g., *ISI Web of Knowledge*, *Scopus*), and the meta-search engine *Google Scholar*. We used standardized search terms to identify sources of information for communal signaling (birds, cooperative signal*/song/singing, communal signal*/song/singing, chorus, chorusing, duet, duetting), territoriality (birds, territor*, year-round territor*, long-term territor*, stable territor*, breeding territor*, flock territor*, non-territor*), and social bonding (birds, social bond*, pair bond*, group bond*, mate retention, mate fidelity, monogamy, divorce; where asterisks (*) denote multiple possible suffixes). Relevant secondary articles were identified from the references cited in books or articles found using these approaches.

Finally, we extended recent efforts (Logue and Hall, 2014) to extract information from sound recordings, images, and videos stored in public and private sound archives to compile evidence of communal signaling, with a focus on Macaulay Library (<http://www.macaulaylibrary.org>), Xeno-canto (<http://www.xeno-canto.org>), and the Internet Bird Collection (ibc.lynxeds.com). Together, these sources contain material for almost all the world's birds. We listened to sound files to verify putative cases of communal signaling and to survey signaling behavior in poorly known species. In addition, we checked accompanying metadata compiled by field recordists for textual confirmation of communal signaling and other details.

Details of methods for assigning species to categories of territory and social bond duration are provided in Appendix A of Supplementary Material. We classified signals as communal with due caution, bearing in mind several alternative possibilities. Distinguishing other multi-individual signals (e.g., contact calls, flock calls, alarm calls, flight calls) was generally straightforward, both in the field and using sound recordings, because these types of acoustic signal are relatively simple, uncoordinated among individuals, and often phylogenetically conserved variations on a theme. We interpreted multi-individual acoustic signals as evidence of communal signaling when they were coordinated or stereotyped. Typical examples include call-and-answer duets, where the gap between songs is shorter and more consistent than in contests between territorial rivals. Similarly, concurrent bursts of acoustic signals from multiple individuals in group-living species often provided a distinctive signature of communal

TABLE 1 | Definitions of response and predictor variables used in statistical analyses.

Variables	Description and categorization
Communal signaling	(1) Non-communal signallers: a species that does not sing communally, only ever as single individuals (2) Communal signallers: a species that produces acoustic signals in groups, either as a duet or chorus
Territoriality	(1) Non-territorial: species that never defend territories, including those that defend very small areas around nest sites, including seabirds, or species where males defend song or display posts only (2) Seasonal or weak territoriality: species with broadly overlapping home ranges, or that habitually join mixed flocks with poorly defined spatial ranges (even those that may defend their position in such flocks) (3) Year-round territoriality: species that defend territories all year, including migrants that are territorial on both the breeding and non-breeding grounds
Social bonds	(1) Solitary: species that does not form pairs, or forms them only briefly during the courtship phase (uniparental care) (2) Short-term pair/group bonds: species with seasonal consorting of pair/group members AND unstable pair/group composition in subsequent breeding attempts [low mate fidelity, high divorce rate (>50% per annum)] (3) Long-term pair/group bonds: species with year-round consorting of pair/group members, or those with seasonal pair/group bonds AND stable pair/group composition in subsequent breeding attempts [high mate fidelity, low divorce rate (<50% per annum)]
Cooperative breeding	(1) Non-cooperative: a species in which no more than two birds, the parents, care for the young (2) Cooperative: a species in which more than two birds habitually care for the young
Migration	(1) Sedentary: does not migrate (2) Partially migratory: minority of population migrates long distances, or most of population undergoes short-distance migration, nomadic movements, distinct altitudinal migration, etc (3) Migratory: majority of population undertakes long-distance migration
Habitat	(1) Open: species primarily occurs in desert, grassland, open water, low shrubs, rocky habitats, seashores, and cities (2) Semi-open: species primarily lives in open shrub land, scattered bushes, parkland, dry or deciduous forest, thorn forest (3) Closed: species primarily lives in tall evergreen forest with a closed canopy, or in the lower vegetation strata of dense thickets, shrubland or marshland
Latitude	Median midpoint latitude as calculated from global range polygons
Mean annual temperature	WorldClim Index BIO1 (C°) averaged across the 1° grid cells corresponding to the breeding distributions defined by global range polygons
Temperature range	WorldClim Index BIO7 (C°) averaged across the 1° grid cells corresponding to the breeding distributions defined by global range polygons
Annual precipitation	WorldClim Index BIO12 (mm) averaged across the 1° grid cells corresponding to the breeding distributions defined by global range polygons
Precipitation range	Difference between WorldClim Index BIO13 and BIO14 (mm), the precipitation of the wettest and driest months respectively, averaged across the 1° grid cells corresponding to the breeding distributions defined by global range polygons

signaling. In practice, assignment to categories was often simplified by the behavioral context of signaling, either directly observed in the field, or reported in sound file metadata. When the context was unclear, we did not necessarily assume communal signaling was occurring when two or more individuals were audible producing long-range acoustic signals, as in many cases it was difficult to rule out counter-singing by individuals in neighboring territories (i.e., different social units).

A separate challenge involves confirming that both males and females are contributing to communal signals. However, in practice this problem was largely irrelevant to socially monogamous species where we assume pairs contain one individual of both sexes. Although scoring species for female song can be challenging when the sexes are monomorphic (Odom et al., 2014), communal signaling is often easier to detect and verify in such cases because both pair members signal in unison. Conversely, it is sometimes difficult to be sure that females are contributing to choruses in group-living species. However, both sexes are known to contribute to choruses in color-marked populations of several species, and the same

message emerges from observations of many monomorphic group-living species in which all individuals can be observed signaling together. Indeed, after considerable attention to this issue, we are not aware of any case of chorusing species where signaling is limited to one sex.

With respect to duetting species, we revised and updated some previous classifications with new information when it was clear that the original reports were based on misinterpretation. Our survey suggested that some species previously listed as duetters should be delisted for the purpose of our analyses because (1) the evidence for communal signaling clearly involved rare or unusual behavior, and (2) literature reports of communal signaling are sometimes based on different definitions of duets and choruses, with these terms often used loosely. For example, some authors use the terms “duet” or “chorus” to refer to counter-calling between neighboring territorial males, or to acoustic signals used in alarm and agitation. One such case is the American Rock-wren *Salpinctes obsoletus*, in which males can produce simple calls during close-quarters agonistic interactions with neighbors, sometimes accompanied by the female, leading to this species

being listed as a duetter (Odom et al., 2015). We re-classify the species as a non-duetter because the calls are short-range signals given in agitation, whereas females do not sing or produce any other long-range signals, either alone or with the male. This distinction is important because males and females of all pair- or group-living bird species occasionally produce short-range acoustic signals at the same time. Counting all such cases as duets will obscure the underlying distribution of conventional duetting, potentially biasing the results of comparative studies, as recently shown in a similar dataset for avian cooperative breeding (Griesser and Suzuki, 2016). Where switches in classification were less certain, we simply assigned a lower score for data quality (see below).

Classifying the world's birds to behavioral and life history categories is challenging, not least because direct information is scarce for many species. We also acknowledge that the boundary between categorical variables is unavoidably blurred, making assignments subjective in some cases. For example, it can be difficult to judge whether a poorly known tropical species is territorial year-round or only during the breeding season, or whether its social bonds endure for a short breeding season or for multiple years (Stutchbury and Morton, 2001). However, for most species there is a growing body of information about local movements and whether particular pairs/groups remain spatially fixed over time. We followed simple rules-of-thumb to classify all cases. When evidence suggested that pairs or groups are highly sedentary, we assumed that pair/group bonds lasted more than a year on average (<50% divorce rate per annum). Our assumption is based on the general pattern established in field studies of color-marked bird populations: we are not aware of any bird species which lives in sedentary pairs or groups year-round and which also has a >50% annual divorce rate. When pair/group bonds break down seasonally (e.g., in migratory species, waterbirds), the uncertainty over divorce rates increases. We assumed that bonds lasted <1 year on average (i.e., >50% pairs or groups that reform in subsequent seasons contain new combinations of individuals) when there is evidence of this outcome in phylogenetically or ecologically related lineages (e.g., many migrant passerines). Conversely, when there was strong evidence that monogamous pairings extended beyond a single breeding season in phylogenetically or ecologically related lineages (e.g., seabirds and many migrant non-passerines), we assumed that >50% pairs reforming over subsequent seasons were likely to contain the same individuals. These procedures may result in some degree of misclassification but we argue that our categories provide an accurate general reflection of variation in social bond duration across the world's birds. Moreover, uncertain cases are reflected in scores of data quality and thus our conservative analyses are restricted to more objective cases.

Finally, assignment to categories may be uncertain when information is drawn from a single locality, or when species vary in a particular trait across their range. Whenever possible, we selected categories on the basis of their predominance in terms of behavior, or their prevalence across the global range of a species. Thus, for example, we classified species as year-round territorial only if such populations made up more than 50% of the global breeding range. In variable or wide-ranging species, we ensured

that predictors and response variables were drawn from the same (or geographically closest) population.

Spatial and Climatic Data

Because communal signaling and the underlying degree of cooperation among individuals may be influenced by latitude and climatic conditions (Rubenstein and Lovette, 2007; Jetz and Rubenstein, 2011; Odom et al., 2014), we used the geographical range polygon for each species to extract median midpoint latitude and environmental data (mean annual temperature, temperature range, annual precipitation, and precipitation range) from the Worldclim database (<http://www.worldclim.org>), following standard methods (Pigot et al., 2010). Species lacking adequate data were excluded for the relevant analyses, leaving a sample of 9230 species for nested taxonomic models. After further excluding species for which no published genetic data yet exist, we retained a sample of 5505 species for phylogenetic mixed models.

For further details of hypotheses and data collection methods, see Appendix A in Supplementary Material; for a complete list of species and sources of information, see Appendices B, C in Supplementary Material.

Data Limitations, Inference, and Uncertainty

In this study, we provide the first global assessment of communal signaling, territoriality, and social bond duration across the world's birds. The scale of this assessment raises a number of challenges, not least because a large proportion of bird species remain poorly known. Nonetheless, we argue that sufficient information is now available to assign almost all species to a useful classification system. To achieve this goal, we used multiple strands of evidence, including direct observations and extensive unpublished information from sound archives and expert field ornithologists. Given the rapid pace of recent ornithological exploration in remote regions, most bird species—aside from a handful of extreme rarities—are now familiar to fieldworkers or birding guides at particular localities where information gathered on repeated visits can provide insight into territorial and social behavior through time. This influx of information is not readily available in published literature, but allows many species previously considered data deficient to be categorized with greater confidence. For example, *Cacicus koepckeae* is excluded from previous literature-based analyses of communal signaling (Odom et al., 2015) but included here as a territorial duetting species on the basis of field observations (Tobias, 2003a) and sound files archived online (see <http://www.xeno-canto.org/species/Cacicus-koepckeae>).

Where evidence was inconclusive, classifications were inferred partly from information relating to multiple close relatives, following standard procedures (Wilman et al., 2014). For communal signals, this type of inference was only used when there were strong grounds for doing so—for instance, when behavior was consistent across close relatives, backed up by circumstantial evidence such as field reports, sound recordings or videos. A similar approach was taken for life history attributes, with estimates of the duration of territory defense or social bonds

often representing a best-guess when sufficient evidence was available from field observations, literature, and related species (see Appendix A in Supplementary Material for full details and rationale). Inferences were never drawn on the basis of phylogenetic relationships alone. Nonetheless, given the scale of our dataset, some lineages are almost certainly misclassified. A detailed summary of possible sources of error is provided in Appendix A of Supplementary Material.

To provide more information about variation in uncertainty, we assigned classifications of all species to four categories of data quality: A, high quality data based on published sources or strongly supported evidence from direct observations; B, medium quality data, including cases where the classification is very likely correct but largely based on field observations and reports; C, low quality data based on few observations, or unsubstantiated literature reports; D, absence of direct evidence. Henceforth, we refer to A as the conservative dataset, B as the medium quality dataset, and C and D together as poor quality data. The degree of inference from congeners is reflected in these categories, from very low inference in A, and minor, supporting inference in B, to larger levels of inference in C. Classifications of data-deficient species (D) were entirely based on inference. Where we found a strong consensus from all strands of evidence, we scored data quality higher than where evidence was in conflict. For example, golden whistlers *Pachycephala pectoralis* are reported to duet in captivity (Brown and Brown, 1994), but this behavior has not been detected in the field. Although this report may use a different definition of duetting to that employed in this study, it nonetheless increases the level of doubt about the lack of duetting observed in congeners, and thus we score most other *Pachycephala* species with an increased level of uncertainty. Finally, because levels of uncertainty often differ for information on communal signaling and general ecology, we scored data quality for both signaling and ecological data separately. Inclusion of species in analyses depended on both signaling and ecological data meeting minimum standards. Species were included (1) in our taxonomic analyses only if they scored A/B for song data quality and A/B/C for life history data quality; (2) in our main (medium quality data) analyses only if they were scored A for song data quality, and A/B for life history data quality; and (3) in our conservative analyses only if they scored A for both signaling and life history data quality. Like all datasets of global scale, ours will undoubtedly benefit from further quality control and curation, and we hope to facilitate this process by archiving all data online in association with this article.

Comparative Analyses

Our analyses included a range of (categorical) behavior and life history variables, and (continuous) climatic variables extracted from geographical ranges. We assessed the effects of these factors on the occurrence and evolution of communal signaling using Bayesian binary-response mixed-effect models with logit link, implemented in the R package, *MCMCglmm* (Hadfield, 2010; Hadfield and Nakagawa, 2010). To account for the potential effects of phylogenetic inertia, we adopted two complementary modeling approaches: (1) Bayesian taxonomic mixed models (BTMM) in which Order, Family and Genus were entered

as nested random factors for all species, and (2) Bayesian phylogenetic mixed models (BPMM), in which phylogenetic relationships were entered as a random factor, assuming a Brownian model of evolution. This random term translates into phylogenetic variance equivalent to Pagel's λ (Pagel, 1999). We included BTMM as this allowed us to include all species with sufficient data ($n = 9230$), whereas BPMM were run on trees obtained from a published multilocus phylogeny, pruned to species with molecular data ($n = 5505$ for the medium dataset; and $n = 1665$ for the conservative dataset; Jetz et al., 2012). We first performed models (BTMM/BPMM) with 11 predictors (10 input variables: 4 intrinsic/life-history and 6 extrinsic/environmental; Table S2). We then re-ran the same models including significant predictors (i.e., those that were statistically significant in both full models) and their second-order interactions. Only interactions with strong effects were included, following (Gelman and Hill, 2007) (see electronic Supplementary Material, Table S3).

For all BTMMs and BPMMs, we used a Gelman prior for random effects (in *MCMCglmm* (Hadfield, 2010) using the command "gelman.prior" (Gelman et al., 2008) with $V = 10^{-6}$, $nu = -1$). We ran three independent runs of *MCMCglmm* for all models, each run for 1.5×10^6 iterations. After discarding a burn-in of 10^6 and a thinning of 5000, the remaining 1000 samples constituted our posterior distribution for each chain. We checked convergence of model parameters (fixed effects and random effects) using the Gelman-Rubin statistic (the potential scale reduction, PSR, factor should be <1.1 among chains (Gelman and Rubin, 1992); all PSR factors met this criterion). We only used posterior distributions from the first of three chains for reporting our parameter estimates (models and 95% credible limits, CLs). Note that in binary models (BTMM/BPMM) a dispersion parameter (akin to residual variance) is unidentifiable (zero). To run the models in *MCMCglmm*, we fixed the parameter > 0 , but then rescaled estimates in the results tables (Table 1, and electronic Supplementary Material Table S1) so that the parameter = 0.

Regression analysis such as BTMM or BPMM are informative about the ecological and social conditions favoring the evolution of communal signaling, but not about the direction of causality. To address this question, we used Pagel's Discrete algorithm implemented in BayesTraits (Pagel and Meade, 2006) to test whether and how key traits have evolved in tandem across the same phylogenetic tree described above. We defined key traits as those significantly correlated with communal signaling in mixed models (BTMM and BPMM). The sample size ($n = 5669$ species) is slightly larger than for BPMMs because fewer species lacked relevant variables. The BayesTraits method uses a likelihood ratio test to compare a model in which the traits evolve independently (independent model) with one in which they evolve in tandem (dependent model). It also estimates the likelihood of evolutionary transitions among traits, assuming correlated evolution. These transition rates provide information about the relative stability of communal signaling with or without a particular life-history trait (and vice versa).

We used this approach to model how communal signaling was associated with territoriality, social bonds and mating system

(independent and dependent models in each case, 6 models in total). As the method can only be applied to binary traits, we dichotomized variables initially classified into three categories (see Table S1). We grouped territoriality into: 1 = species with year-round territoriality, 0 = weak/seasonal territoriality or non-territorial. Similarly, we dichotomized social bond duration into: 1 = long-term (>1 year) pair/group bonds, 0 = short-term pair/group bonds or non-sociality. We grouped traits in this way for two main reasons. First, it produces the most balanced sampling in a dichotomous framework because relatively few species are non-territorial or lack social bonds (Figure 3). Second, this division most closely reflects existing hypotheses for communal signaling, which point to the importance of year-round territoriality (Benedict, 2008) and social stability (Logue and Hall, 2014).

We ran each BayesTraits model for 1.1×10^7 iterations, discarding an initial burn-in of 10^6 and sampling the chain every 10,000 iterations, resulting in a sample of 1000 per model/per tree. We ran two independent chains on each tree in the sample and combined samples resulting from all the runs, which constituted our posterior distributions for all parameter estimates. In all cases, a hyper prior of an exponential distribution (seeding from a uniform distribution on the interval 0–100) for a reversible jump procedure (see <http://www.evolution.rdg.ac.uk/BayesTraits.html>). The trees were scaled by 0.05, as the rates are proportional to the branch lengths. This places the transition rates on a more usable scale and does not alter their relative values. For each chain, the marginal likelihood was calculated using a stepping stone sampler (Xie et al., 2011): 100 stones were distributed according to a beta distribution (shape 0.400000, scale 1.000000) and each stone was run for 25,000 iterations.

RESULTS

Prevalence and Distribution of Communal Signaling

We found evidence of communal signaling in 1830 species (18%) in the total list of 10328 species (see Appendix A in Supplementary Material). Excluding species with poor signaling data (category C and D) produced a smaller total of 1812 species with communal signaling (17%); of these, duetting occurs in 1627 (~16 %) species, a total that includes chorusing species which occasionally duet. Duetting was previously thought to be present in only 222 (or ~2–3%) of species (Thorpe, 1972; Kunkel, 1974; Farabaugh, 1982; Hall, 2004), with the estimate recently revised to 420 species (~4%; Hall, 2009). Even excluding species with poor quality data (categories C and D), our results indicate that communal signaling is taxonomically widespread, evolving multiple times across the avian tree of life (Figure 1), occurring in 26/39 orders (67%) and 110/225 families (49%), with roughly equal prevalence in the passerines (1102/6049, 18%) and non-passerines (710/3522, 20%).

Our data confirmed that the geographical distribution of communal signaling is uneven, with greatest prevalence in western Amazonia, western and central Africa, Indo-Malaya, and northern Australia (Figure 2A). This distribution remains

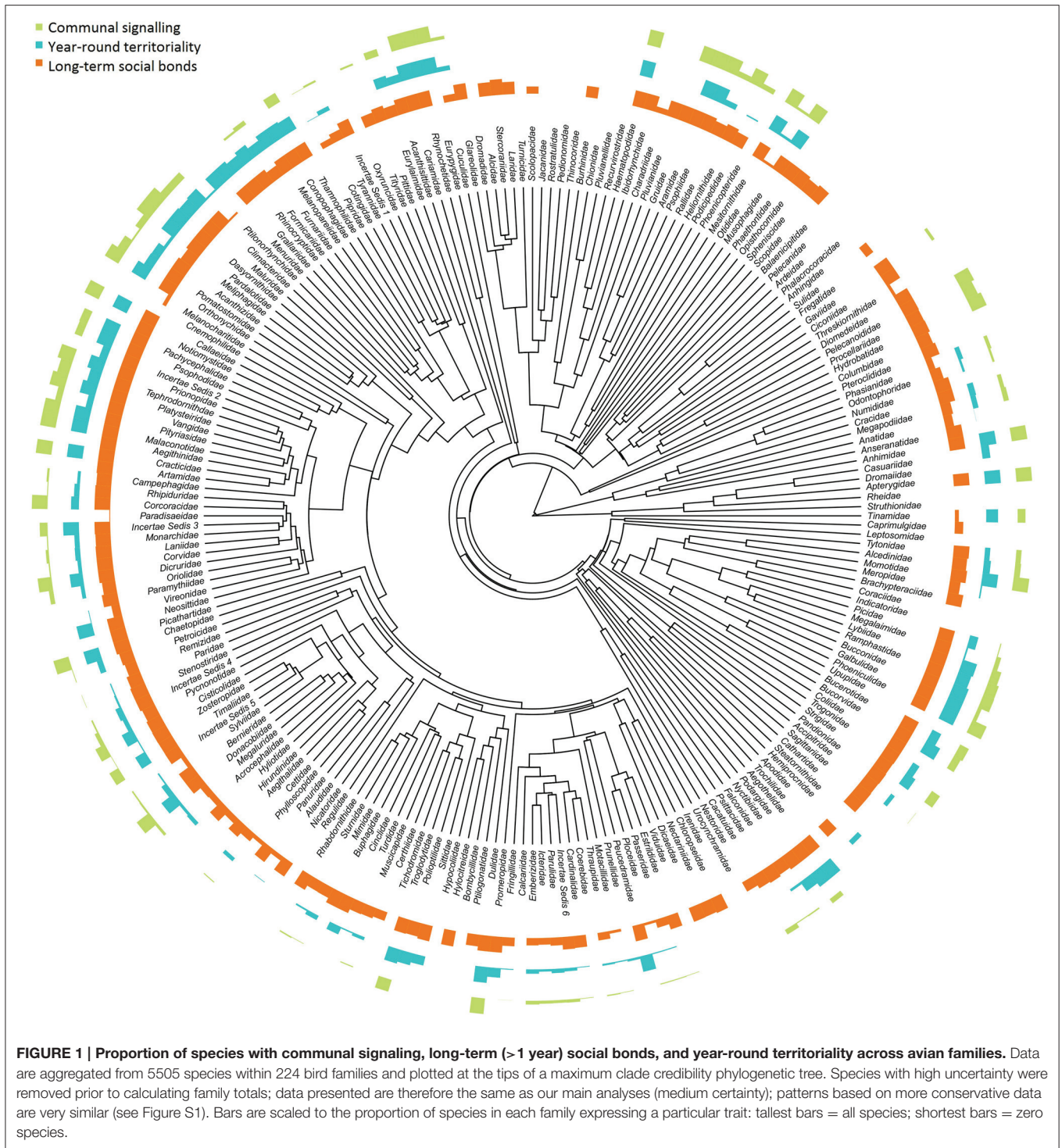
essentially unchanged when focusing on duetting species (Figure 2B) and conservative data (Figure S2). In general, more duetting and chorusing species occur in the tropics (Figures 2, 3A). However, this pattern is largely driven by greater species richness in the tropics, and after correcting for the gradient in overall diversity we find that communal signaling peaks in the southern hemisphere (Figure 3A). Across the world's terrestrial biomes (Olson et al., 2001), the highest proportions of species with communal signaling (18–20%) occur in tropical and subtropical habitats (grasslands, savannas, shrublands, and both moist and dry broadleaf forests), while the smallest proportions (~6%) occur in tundra and boreal forests (Table S1).

Predictors of Communal Signaling

We found that there is a strong phylogenetic signal in the occurrence of duetting and chorusing (Figure 1), with evolutionary history a dominant predictor of these traits in our combined full (Table S2), and final models (Table S3). In the BTMM, taxonomy (Order, Family, Genus) explained 16–39% of the variance in communal acoustic signaling, and in the BPMM, phylogeny explained ~96% of variance (at both levels of data certainty we used in analyses; see below). This result is not surprising given that communal signaling is widespread in some clades (e.g., antbirds *Thamnophilidae*) but absent in others (e.g., hummingbirds *Trochilidae*). However, the strength of phylogenetic signal may be inflated because we sometimes inferred shared character states among close relatives. We note that (1) even a much weaker phylogenetic signal supports our assumption of a Brownian motion model of evolution in subsequent analyses, and (2) inference of shared character states among relatives does not affect our main results because we use both taxonomic (BTMM) and phylogenetic (BPMM) models to correct for phylogenetic non-independence when testing for associations with communal signaling.

We found that territoriality, social bonds, cooperative breeding, latitude, and temperature range were all significant predictors of communal signaling in BTMMs (Tables S2, S3). No such association was found between habitat density or migration and communal signaling. However, the results of this hierarchical model should be treated with some caution because the BTMM contains only basic evolutionary information and may therefore fail to account adequately for phylogenetic non-independence (pseudoreplication).

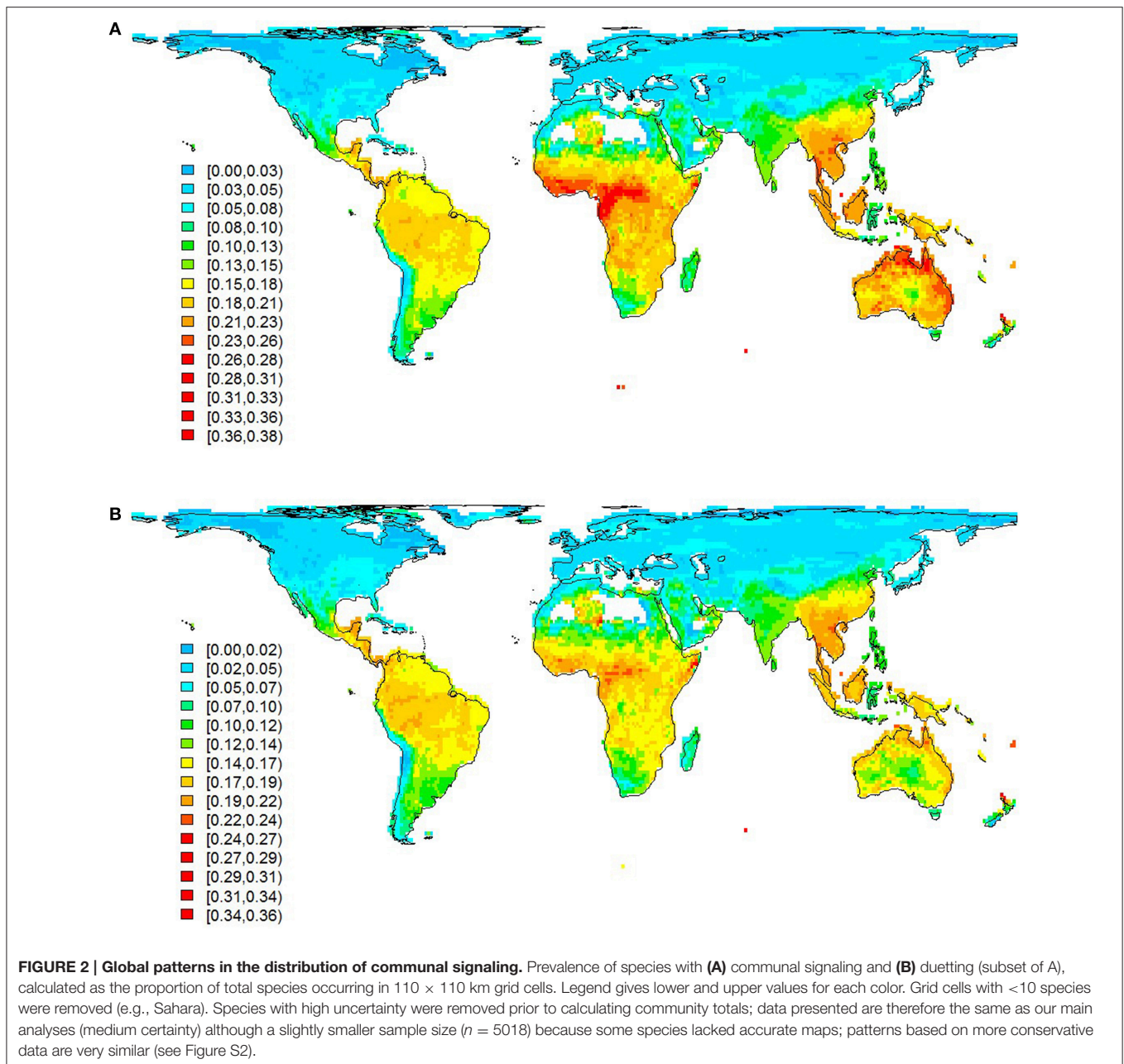
Table S4 When we re-analyzed our data using BPMM, thus controlling for phylogeny, we found that communal signaling was significantly associated with territoriality and social bond stability, and that cooperative breeding was the only other significant (but weaker) correlate. We note that territoriality and cooperative breeding are strongly correlated: a model predicting cooperative breeding as a function of territoriality has an overall estimated R^2 of 0.956, with an estimated partial R^2 of phylogeny of 0.954; the coefficient estimate for the scaled territoriality value is -1.849 (CI: $-2.677, -1.172$). In contrast, we found no evidence that latitude, habitat density, migration, or climatic variability were associated with communal signaling (Tables S2, S3). Thus, although species with duets and choruses appear to be



more prevalent in relatively stable tropical habitats (**Figure 2A**) with low annual variation in temperature (**Figure 3B**) and rainfall (**Figure 3C**), these associations disappeared when we accounted for evolutionary relationships and life-history traits. Running BPMMs on conservative data produced very similar results, except that the relationship between cooperative

breeding and communal signaling then becomes non-significant (Table S2).

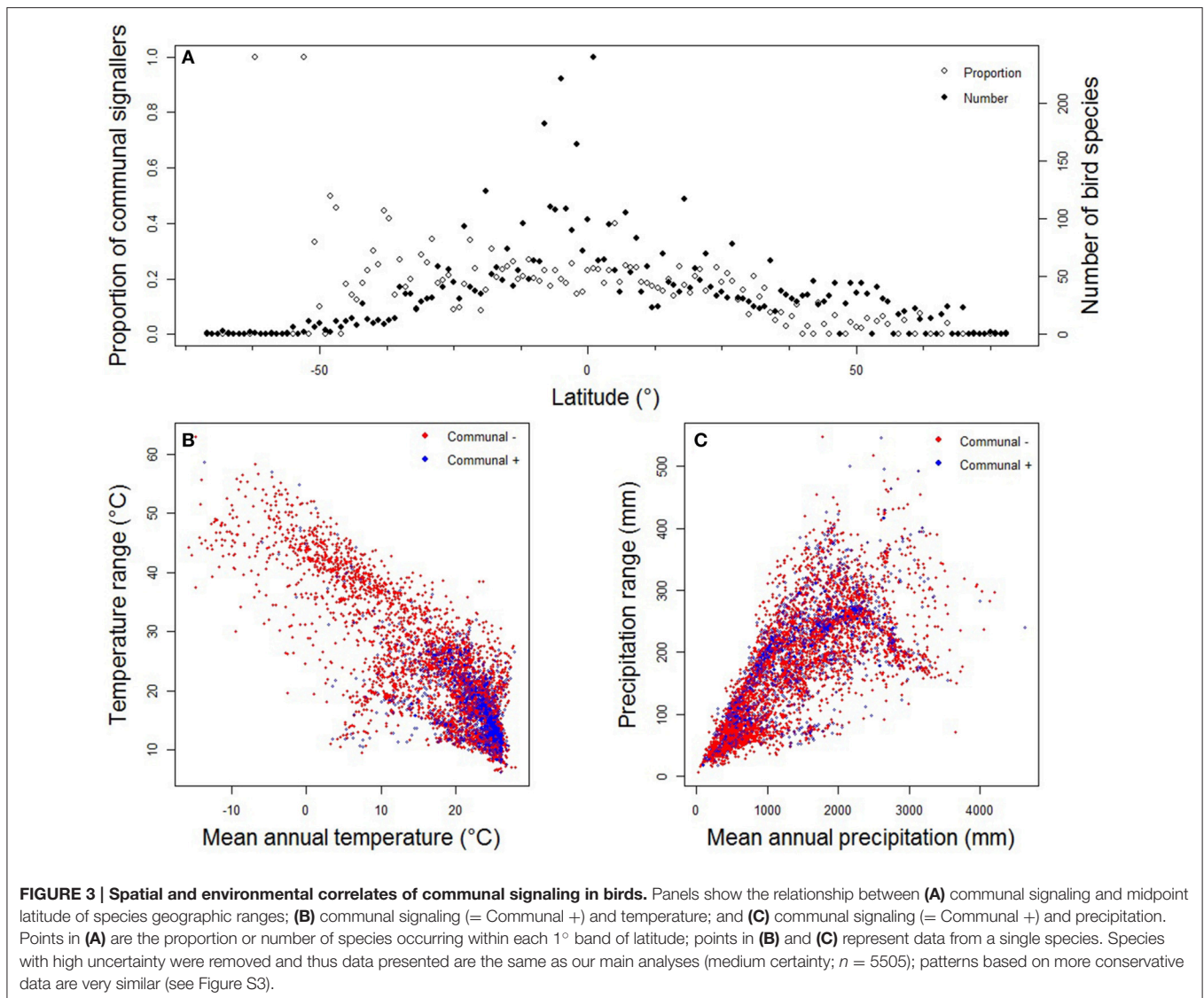
The fact that year-round territoriality and long-term social stability emerge as the most important predictors of communal signaling seems to make sense because many duetting or chorusing species share both these life history traits (**Figure 4**).



However, the underlying correlation between territoriality and sociality is accounted for by our mixed modeling approach, and in any case the relationship between them was highly asymmetric: 3010 species with both strong territoriality and long-term social bonds made up 97% of the 3096 species with strong territoriality, but only 40% of the 7556 species with long-term social bonds. We also detected a significant interaction between territoriality and sociality (Table S3). Specifically, our results suggest that having one or other of year-round territoriality or social stability has a very large effect on the probability of communal signaling, particularly in the case of year-round territoriality, but that it's less important to have both (Table S3).

Co-Evolution of Communal Signaling with Life-History Traits

When we used BayesTraits analyses to examine evolutionary transitions between states, we again found strong evidence that communal signaling evolved together with year-round territoriality (average log Bayes Factor 824.66), stable social bonds (average log Bayes Factor 310.70) and, to a lesser extent, cooperative breeding (average log Bayes Factor 26.23; Tables S4, S5). A log Bayes Factor above two can be viewed as significant (Kass and Raftery, 1995). Re-running these analyses on conservative data produced similar results (Tables S4, S6). The associations were slightly weaker (although still very strong) between communal signaling and both year-round territoriality



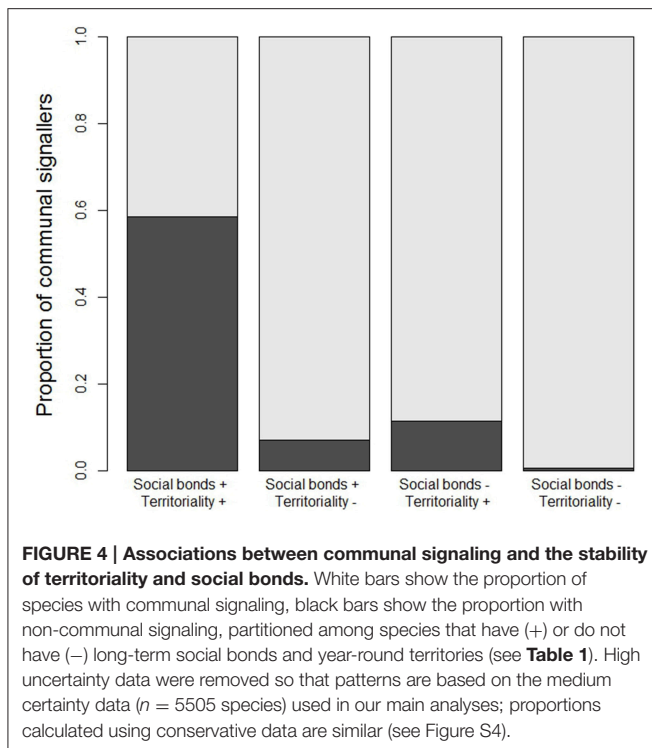
(average log Bayes Factor 528.69) and stable social bonds (average log Bayes Factor 229.81). However, the significant association between communal signaling and cooperative breeding in the conservative dataset was much lower (average log Bayes Factor 6.29) and not significant in every tree (91 out of 100 had a Bayes Factor > 2).

Figure 5 illustrates the flow between evolutionary states detected in BayesTraits analyses. The arrows depicting this flow provide information about the stability of evolutionary states, with a low transition rate toward and a high transition rate away from a particular state indicating low stability of that state. For example, in (C) State 3 (communal signals and weak social bonds) is highly unstable, readily transitioning to State 1 (solo signals and weak social bonds) or State 4 (communal signals and strong social bonds). Similarly, the co-occurrence of communal signaling with cooperative breeding is unstable, readily transitioning to state 3, where breeding is non-cooperative but signaling is communal (**Figure 5D**). Conversely, in (B),

State 4 (communal signals and strong territoriality) is stable, with balanced transitions to and from State 2 (solo signals and strong territoriality), and State 3 (communal signals and weak territoriality). The key points to take from **Figure 5** are that q24 (evolving communal signals with territoriality) occurs 20 times faster than q13 (evolving communal signals without territoriality; **Figure 5B**), and that q34 (evolving communal signals with social bonds) occurs 23 times faster than q12 (evolving social bonds without communal signals; **Figure 5C**; Table S5).

DISCUSSION

Our comparative analyses reveal that avian duets and choruses are significantly linked to both year-round territory defense and long-term social bonds, and only weakly associated with cooperative breeding. Furthermore, once we accounted for these relationships, as well as for shared ancestry, we found no



evidence that latitude, climatic variability, habitat, or migration predicted the occurrence of communal signals. These findings are corroborated by patterns of co-evolution among key life-history traits, which indicate that the presence of duets and choruses is most stable in association with territoriality and sociality. Thus, our results suggest that social factors predominate over environmental factors in driving communal signal evolution, and that the intensity and duration of ecological resource defense coupled with social stability provides the most general explanation for communal signal evolution.

The advantage of our broad-scale approach is that it offers sufficient statistical power to compare the effects of multiple factors. Our results shift the emphasis away from previously identified correlations with latitude, habitat density, migration, and climatic variability, perhaps because earlier studies were based on relatively restricted datasets sampled inconsistently across latitudes, climates, or major clades (e.g., passerines vs. non-passerine). This patchy sampling may generate different outcomes because associations vary across clades and contexts. For instance, while it is clear that for some species duets function partly in maintaining contact between pair members in dense habitats (Mennill and Vehrencamp, 2008), many duetting species occur in open environments, implying that habitat density does not provide a general explanation for communal signaling.

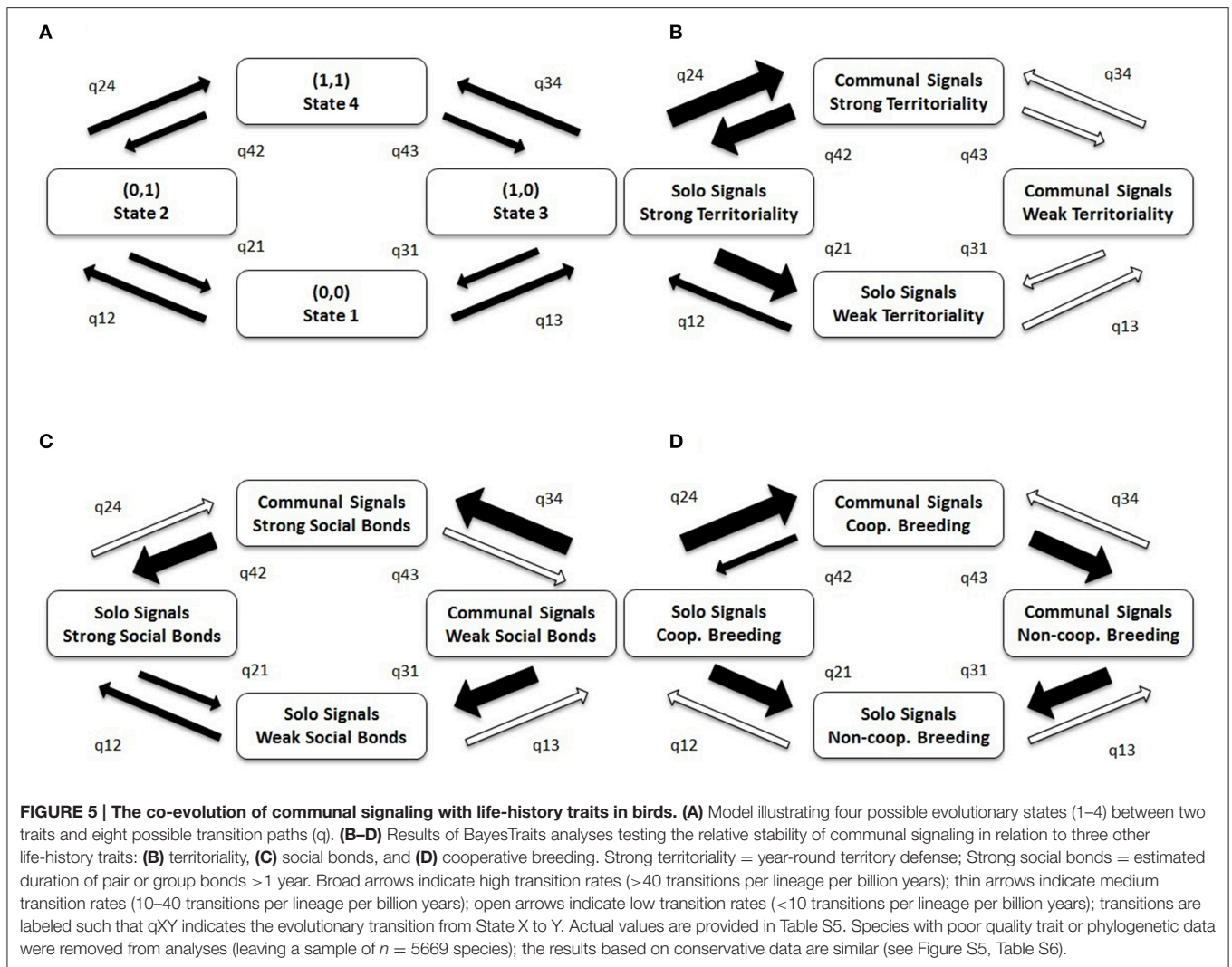
By sampling across the full span of environmental and life history variation in the world's birds, we have shown that correlations between communal signaling and environmental (extrinsic) factors are consistently subordinate to correlations with life-history (intrinsic) factors. The importance of species ecology over environmental conditions in promoting communal signaling has not previously been reported, but fits the

observation that duets are well known in temperate zone species with year-round territoriality (e.g., tawny owl *Strix aluco*) or long-term social bonds (numerous seabirds), as well as in tropical species with the same underlying traits. Rather than latitude or climate explaining patterns in signaling behavior, our results suggest that the uneven geographical distribution of communal signaling shown in Figure 2 arises simply because extended forms of territoriality and sociality are biased toward the tropics and southern hemisphere. Indeed, this effect has been reported within evolutionary lineages: in the house wren *Troglodytes aedon* complex, for example, communal signals are common in the tropics where territories are defended year-round, but rare in the temperate zone where territoriality is seasonal (Stutchbury and Morton, 2001).

Selection is likely to favor long-term territoriality and social bonds at low and southern latitudes for a number of reasons (Jankowski et al., 2012; Tobias et al., 2013). First, the climate is generally more stable than in the northern temperate zone (Ghalambor et al., 2006), promoting sedentary lifestyles and stable social bonds. Second, the year-round availability of many ecological resources (Huston and Wolverson, 2009) means that the territories of land-birds are worth defending over longer time-periods. Third, avian populations in the tropics often approach carrying capacity owing to reduced mortality and increased longevity (Wiersma et al., 2007; Williams et al., 2010). Together, these factors place a high premium on the collaborative defense of ecological resources and group membership in the tropics, as territory or group vacancies are theoretically scarce and difficult to regain if lost. In this context, individuals may signal communally to protect their positions in long-term coalitions, which in turn cooperate over signal production to deter rival pairs or groups.

Disentangling the role of territoriality and sociality is challenging because communal signaling frequently occurs in conjunction with both year-round territoriality and long-term social bonds, which often occur together (Figure 4). This connection between long-term territoriality and social cohesion suggests that competition for ecological resources increases in parallel with competition over membership of partnerships or coalitions of individuals, perhaps helping to explain why avian duets appear to mediate both cooperation (i.e., joint territory defense; Seddon and Tobias, 2003; Hall and Magrath, 2007) and conflict (i.e., mate-defense; Sonnenschein and Reyer, 1983; Rogers et al., 2007; Tobias and Seddon, 2009). Nonetheless, phylogenetic mixed models revealed that the effect of territoriality was more than twice as strong as that of social bonds (Tables S2, S3), whereas cooperative breeding was only weakly associated, with an effect approximately one quarter that of social bonds.

Similarly, the evidence from evolutionary transitions suggests that the combination of year-round territoriality and communal signaling is a more stable state, and far more likely to co-evolve, than long-term social bonds coupled with communal signaling (Figure 5, Table S5). Furthermore, the BayesTraits analyses provide a clue that territoriality may be crucially important as a precursor to communal signaling, whereas long-term social bonds in pairs or groups may actually arise after communal



signaling evolves—that is, pair and group bonds may result from selection for defending resources as a coalition, rather than vice versa. Although the pattern of evolutionary transitions in our dataset is most consistent with this interpretation, we do not specifically reconstruct ancestral states, and so the question of evolutionary pathways to (and from) communal signaling requires further investigation.

Many cooperatively breeding birds appear to signal as a group, and thus our finding that cooperative breeding is only weakly associated with communal signaling is perhaps surprising. The reason for this outcome becomes clearer when considering the correlation between cooperative breeding and territoriality, which is both strong and largely explained by phylogeny. Of these two associated variables, our results indicate that cooperative breeding is a much weaker predictor of communal signaling, and thus when territoriality is accounted for in phylogenetic models, cooperative breeding has very little additional explanatory power. This is particularly evident in our conservative analyses, where the association between cooperative breeding and communal signaling is removed altogether.

Cooperative breeding is only one form of cooperation in birds, and almost all avian duets and choruses function at least partly in cooperative contexts (Dahlin and Benedict, 2014), suggesting that global patterns of communal signaling can shed light on the evolution of cooperation (Logue and Hall, 2014). In highlighting the importance of long-term social bonds, our findings echo those of previous studies on duetting (Benedict, 2008; Logue and Hall, 2014). Moreover, as pointed out by Logue and Hall (2014), this pattern aligns with theoretical (Trivers, 1971) and empirical studies (Heide and Miner, 1992; Bó, 2005) suggesting that cooperation among individuals is most likely to arise when they associate over prolonged periods. Previous explanations for this effect are mainly based around the concepts of trust, reciprocity or kin selection (Heide and Miner, 1992). However, while it is difficult to rule out the influence of these factors in our study, the abundance of communal signals in species that are either socially monogamous or group-territorial with low intra-group relatedness suggests a prominent role for the simpler theory of interdependence (Roberts, 2005). Under this view, individuals cooperate over signal production because of

the direct fitness benefits of collaboration—that is, individuals are more likely to maintain positions in pairs or groups and to defend adequate resources to reproduce if they coordinate signaling as a team.

Challenges and Opportunities

Synthesizing current information on territorial behavior, social stability and communal signaling across the world's birds is difficult given the lack of published studies for most species. Nonetheless, by incorporating multiple strands of evidence, including direct observations, experiments, and expert knowledge, we believe our dataset provides the most robust and comprehensive estimate of current knowledge to date. Our classification of species into broad categories means that, although some error is unavoidable, the majority of lineages are very likely assigned correctly. Moreover, the sample size is large enough to absorb considerable noise and we suspect that the key patterns reported are so striking that future adjustments will have little influence on the main results. This conclusion is strongly supported by sensitivity analyses showing that our results are robust to variation in data quality.

In effect, we have followed the model adopted by many prominent studies of climate change, or the IUCN Red List categories of conservation status (IUCN, 2001). The Red List uses arbitrary thresholds to assign species to threat categories in all but the most data-poor scenarios, often on the basis of expert opinion. Despite the drawbacks and early criticisms of this approach, it has been shown to be largely accurate, and has proved to be an extremely valuable tool for a prolific field of research (Rodrigues et al., 2006). While further revisions and corrections are inevitable, we hope the classifications presented here provide a similar template for further study, both to refine the dataset and to underpin broad-scale tests of evolutionary theory, in line with previously published datasets of similar scope (Cockburn, 2006; Jetz and Rubenstein, 2011; Wilman et al., 2014).

CONCLUSIONS

Based on our global survey, we estimate that communal signaling occurs in at least 1830 (~18 %) bird species, and is thus far more widespread than often assumed. Our analyses confirm that the occurrence of this behavior across the world's birds is correlated with a suite of environmental variables, including climatic variability and latitude, as well as migratory behavior and cooperative breeding. However, all these associations appear

to be secondary because they are largely or entirely explained by a combination of long-term territory ownership and social bonds. We propose that the value and defendability of ecological resources, and the fluctuation of their value and defendability over time, are key factors driving the evolution of communal signaling. Competition for defendable resources may promote the formation of stable coalitions, theoretically increasing the degree of interdependence and collaboration among individuals. Given that communal signals are by definition produced by females as well as males, it seems likely that similar processes also play a prominent role in maintaining songs in females. However, further studies are required focusing more explicitly on patterns of female song in birds, including species where females sing independently from males.

AUTHOR CONTRIBUTIONS

JT and NS conceived, designed, and coordinated the study, and wrote the manuscript. JT and AC compiled and curated data. CS, AM, and SN designed and carried out statistical analyses.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://journal.frontiersin.org/article/10.3389/fevo.2016.00074>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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