**Title:** Dawn Singing of the Brownish-Flanked Bush Warbler Influences Dawn Chorusing in a Bird Community

Short running title: interspecific influences dawn singing

Authors: Canwei Xia\*, Huw Lloyd†, Jie Shi\*, Chentao Wei\* & Yanyun Zhang\*

# Author's institutional affiliations:

\* Ministry of Education Key Laboratory for Biodiversity and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing, China
† Division of Biology and Conservation Ecology, School of Science and the

Environment, Manchester Metropolitan University, Manchester, UK

**Correspondence:** Yanyun Zhang, Ministry of Education Key Laboratory for Biodiversity and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing, 100875, China. E-mail: zhangyy@bnu.edu.cn

**Acknowledgements:** We thank Prof. Anders Pape Møller and Dr. Lu Dong for helpful comments. This work was supported by the National Natural Science Foundation of China (No. 31601868) and the Beijing Natural Science Foundation (No. 5173030). All aspects of this study were approved by the National Bird-banding Center of China (NBCC) under license number H20110042 and the local administrator of the Dongzhai National Nature Reserve under permit number 2011002.

Authorship: Canwei Xia and Yanyun Zhang conceived and designed the experiments. Chentao Wei collected the data. Jie Shi analyzed the data. Canwei Xia, Huw Lloyd and Yanyun Zhang wrote the manuscript.

**Conflict of Interest Statement:** The authors declared that they have no conflict of interest to this work.

**Abstract:** Despite numerous studies on the function of the avian dawn chorus, few studies have examined whether dawn singing may influence the singing of other species. Here, we built on our previous study which found male Brownish-flanked Bush Warblers (*Horornis fortipes*) increase their dawn singing intensity after conspecific playback on the previous day. We reanalyzed those recordings to quantify the start of dawn singing in other 9 sympatric songbird species. Ranking-scaling analyses identified a distinctive sequential pattern of dawn singing among these bird species between the first and the second dawn chorus, and meta-analysis showed a significant

trend to singing earlier in the bird community accompanied by the increase in dawn singing intensity in Brownish-flanked Bush Warbler. Species with songs most similar to that of the Brownish-flanked Bush Warbler and species that were phylogenetically distantly related to the Brownish-flanked Bush Warbler showed a greater shift in the onset of dawn singing. Our study is one of the few studies showing how bird song influences heterospecific singing, and this may influence the temporal organization of song activity in the community, and result in synchronization in singing activities among different species, such as singing in dawn and dusk chorus.

**Key words:** dawn chorus, heterospecific song, interspecific influences, meta-analysis, ranking-scaling analyses, social information

#### Introduction

Social information has been shown to benefit conspecifics, but can also be used interspecifically. For example, migrant flycatchers (e.g. Collard Flycatcher Ficedula albicollis and European Pied Flycatcher Ficedula hypoleuca) are known to use social cues of resident birds (e.g. Great Tit Parus major and Blue Tit Cyanistes caeruleus) as a source of information regarding the quality of potential nest sites (Kivela et al., 2014; Seppanen & Forsman, 2007; Seppanen et al., 2011). Among bird acoustic signals, alarm calls and mobbing calls are perhaps the best known sources of interspecific social information (Haff & Magrath, 2013; Magrath et al., 2015; Munoz et al., 2015). Playback experiments have revealed that White-browed Scrubwrens (Sericornis frontalis) and Superb Fairy-wrens (Malurus cyaneus) flee to dense vegetation cover following playback of either species' alarm calls (e.g. Fallow et al., 2011; Fallow et al., 2013). Another kind of bird acoustic signal - bird song - is generally assumed to affect only conspecifics, because the main function of bird song serves to attract mates (conspecific females) and to deter conspecific territorial (male) rivals (Kroodsma & Byers, 1991; Slater, 2003). An ecologically wide array of different bird species increase their singing activity in response to heterospecific playback (Møller, 1992), but most studies have attributed these responses to the similar song features among sibling species (Martin & Martin, 2001; Reif et al., 2015) or interspecific competition among species with similar niches (Gorissen et al., 2006; Grava et al., 2012). Two recent studies have suggested that songbirds may use heterospecific songs as cues to acquire social information. DeJong et al. (2015) found that non-focal species respond to heterospecific playback by decreasing their use of the habitat around the playback sites. Schepers & Proppe (2016) found that heterospecific playback of the songs of 6 different bird species causes a significant increase in the territorial density of 11 additional (nonfocal) species. Despite these findings, it remains difficult to evaluate whether the influence of the non-focal species is due to the playback of heterospecific song or

interspecific competition for resources, because territorial density and habitat use by some focal species has been found to increase at playback sites (DeJong et al., 2015).

Bird song is most intensely used during the dawn period, when most diurnal bird species typically sing with high song rates (Burt & Vehrencamp, 2005; Staicer et al., 1996). The onset (timing) of dawn singing is often influenced by several environmental and biological factors. Birds are known to begin singing earlier with increasing overnight temperature and light intensity (e.g Barnett & Briskie, 2007; Hutchinson, 2002; York et al., 2014). Human activities may also influence dawn singing, because artificial night lighting and traffic noise can result in earlier singing of birds in cities (e.g. Gil et al., 2015; Silva et al., 2014; Silva et al., 2016). As song can attract predators, birds tend to reduce their song output and stop singing earlier when predators appear (Schmidt & Belinsky, 2013). Biological factors, such as eye size (e.g. Berg et al., 2006; Thomas et al., 2002), reproductive stage (e.g. Hamao, 2008; Poesel et al., 2006) and interactions among conspecifics (e.g. Foote et al., 2010; Foote et al., 2011; Stehelin & Lein, 2014) can influence the timing of dawn singing. Staicer et al. (1996) proposed the social dynamics hypothesis, which emphasizes that the function of the dawn chorus is interactive communication and adjustment of the social relationships between conspecific males. Experimental evidence has shown that the onset of dawn singing can significantly change following territorial intrusions (e.g. Amrhein & Erne, 2006; Erne & Amrhein, 2008) with the earliest timing of dawn singing made by males with many neighbours (e.g. Sexton et al. 2007). Although there have been numerous studies on dawn chorus, studies on the influence of heterospecific song on dawn singing are lacking.

In a previous study (Xia et al., 2014), we recorded dawn singing by 21 different Brownish-flanked Bush Warbler (*Horornis fortipes*) males on two continuous days. We randomly selected 12 males and used playbacks as simulated territorial insertions on the afternoon of the first day. We found that, in agreement with the prediction of the social dynamics hypothesis (Burt & Vehrencamp, 2005; Staicer et al., 1996), these 12 males increased their dawn singing intensity (singing earlier and with a higher rate) on the second day, whereas the other 9 males did not. In this study, we reanalyzed these recordings to quantify the start of dawn singing by other sympatric songbird species. Since bird song can be used to transmit cues for predator absence (e.g. Møller, 1992), and birds preferentially sing in the absence of predators (e.g. Schmidt & Belinsky, 2013), we predicted that a temporal shift in the onset of dawn singing in the community was influenced by Brownish-flanked Bush Warbler singing. Response toward heterospecific song is reported between species with similar song features (Reif et al., 2015), similar niches (Gorissen et al., 2006; Grava et al., 2012), or among sibling species (Martin & Martin 2001). Thus, we also predicted species whose songs or niches are more similar to that of the Brownish-flanked Bush Warbler, and species that are closely phylogenetically related to the Brownish-flanked Bush Warbler show a greater shift in the onset of dawn singing.

## Methods

#### Study area and bird song recordings

Fieldwork was conducted in the Dongzhai National Nature Reserve, Henan province, southern China (31.9°N, 114.3°E). The reserve is dominated by mature montane forest habitats at 100-466 m elevation interspersed with small tea plantations, villages, and a small network of public trails. From April 8th to April 13th, 2011, we recorded the dawn chorus singing of 21 different territorial Brownish-flanked Bush Warbler males across two consecutive days, by placing the recorder near the center of each territory. The farthest song posts of these males were  $30 \pm 10.1$  m (mean  $\pm$  SD; range: 17 to 60 m) from the center of their territories where we placed our recorder (Xia et al., 2014). Individuality of Brownish-Flanked Bush Warbler male can be identified by song spectrograms, as each male has unique song features (Xia et al., 2012). Recording sites were separated by a minimal distance of 150 m, and some territories were situated much further apart in different valleys. All dawn chorus recordings were made in WAV format (44.1 kHz, 16 bit) using Tascam DR-07 portable digital recorders (Tascam Co., Tokyo, Japan), placed near the center of each Brownish-flanked Bush Warbler's territory. Recordings were made from 5 a.m. to 8 a.m. (time zone: GMT + 8 h), corresponding to approximately 1 h before sunrise before any diurnal bird species start to sing at the study area and 2 h after sunrise. All focal Brownish-flanked Bush Warbler males were randomly divided into an experimental group (12 males) and a control group (9 males) by using a coin toss. For the experimental group, we played back 15 min of Brownishflanked Bush Warbler song as simulated territorial insertion on the afternoon of the first day, between 2 p.m. and 6 p.m., whereas the control group was not exposed to any playback treatment. More details on the fieldwork protocols are provided in Xia et al. (2014).

## Time of dawn singing

We used Avisoft-SASLab Pro 4.3 software (Avisoft Bioacoustics, Berlin, Germany) to create spectrograms with the following settings: resampling frequency, 22.05 kHz; sample size, 16 bits; fast Fourier transform length, 256 points; hamming window, frame size of 100% and overlap of 50%; frequency resolution, 86 Hz; and time resolution, 5.8 ms. Species singing during the dawn chorus were identified the spectrograms by one of the authors (Shi, J.), who is highly trained in bird song identification and is familiar with all species in the study area. The time of dawn singing, for each species at each

recording site, was defined as the first song of this species in this recording site minus the time of sunrise. Thus, a negative value indicated that a species sang earlier than sunrise.

The songs of 16 bird species were recorded during the study period; 6 of these species were excluded from subsequent analyses (Red-billed Blue Magpie Urocissa erythrorhyncha, Common Magpie Pica pica, Eurasian Jay Garrulus glandarius, Silky Starling Sturnus sericeus, Scaly Thrush Zoothera dauma, and Pallas's Leaf Warbler Phylloscopus proregulus) because their songs were present in either the control or experimental recording groups, but never in both groups. Recordings of the remaining 10 species (Yellow-bellied Tit Parus venustulus, Great Tit Parus major, Rufous-necked Scimitar Babbler Pomatorhinus ruficollis, Spectacled Laughingthrush Garrulax perspicillatus, Hwamei Garrulax canorus, Vinous-throated Crowtit Paradoxornis webbiana, Collared Finchbill Spizixos semitorques, Red-headed Tit Aegithalos concinnus, Brownish-flanked Bush Warbler Horornis fortipes), and Blackbird Turdus *merula*) were used in the analysis. The number of recording sites for these species range from 6 (Blackbirds) to 19 (Hwamei and Vinous-throated Crowtit). Males of all these species were establishing territories and engaged with attracting mates during the time of this study except for Red-headed Tit, which were feeding nestlings (e.g. Li et al.,2012).

## Phylogenetic data

Phylogenetic data for all 10 target species were obtained from Jetz et al. (2012), which is currently recognized as the most comprehensive source of phylogenetic information on birds. We followed a similar approach as Brouwer et al. (2017) and Medina et al. (2017), and downloaded 1000 trees from www.birdtree.org, all of which represent samples from a Bayesian estimate of the phylogeny of all bird species. Then we compiled them into a maximum clade credibility tree using Tree Annotator in BEAST v1.8.3. Phylogenetic distances to the Brownish-flanked Bush Warbler were calculated from the maximum clade credibility tree (Figure 1).

## Song measurements and niches

To calculate the song similarity, we measured 5 songs per individual, and three individuals for each species (Figure 2). These songs were recorded using a TASCAM HD-P2 portable digital recorder (Tascam Co., Tokyo, Japan) and a Sennheiser MKH416 P48 external directional microphone (Sennheiser Co., Wedemark, Germany). Each song consisted of several notes, with pauses of at least 1 s between songs. A note was defined as a continuous signal within a spectrogram. For each song, we measured 6 variables: maximum frequency, minimum frequency, peak frequency, duration of song,

number of notes, and number of different notes. Peak frequency refers to the frequency associated with the maximum energy. We ignored harmonic components when measuring frequency, because it was difficult to set a standard to measure harmonic components because their amplitude was observed to gradually decrease.

Following Soberon (2007) and Olalla-Tarraga et al. (2017), we describe (Eltonian) niches based on resource consumer, using the information of diet and foraging strata from Wilman et al. (2014), widely considered to be the most comprehensive source of (Eltonian) niche data for birds. Brownish-flanked Bush Warbler mainly forage on invertebrates on the ground and in low-lying bushes, similar to Rufous-necked Scimitar Babbler, Spectacled Laughingthrush, Hwamei, Red-headed Tit, and Blackbird; while Yellow-bellied Tit, Great Tit foraging on invertebrates in trees, and Vinous-throated Crowtit and Collared Finchbill mainly foraging on seed and fruit. So, we separate species into two groups: with or without similar niches as the Brownish-flanked Bush Warbler. The former includes Rufous-necked Scimitar Babbler, Spectacled Laughingthrush, Hwamei, and Blackbird, while the latter includes Yellow-bellied Tit, Great Tit, Vinous-throated Crowtit, and Collared Finchbill.

## Statistical analyses

We used ranking-scaling (RASC) analysis (Agterberg & Gradstein, 1999) to identify the sequential order of the onset of dawn singing by different species. RASC produces a single, comprehensive ordering of events, even if the data contain contradictions in different samples of observations, by producing a 'majority vote', i.e., counting the number of times each observation occurs above, below or together with all other observations (Agterberg & Gradstein, 1999). RASC estimates 'distances' between the consecutive observations or events by counting the number of observed relationships between each pair of consecutive observations. A small number of contradictions suggests a greater distance between those observations. RASC analysis was performed using Past 3.06 software (Hammer et al., 2001) on all recordings from 21 sites in the first dawn period to identify the sequential ordering of the onset of dawn singing by different species before playback, and on recordings from 12 sites (which were done as simulated territorial intrusions during the previous afternoon) in the second dawn period to identify the sequential order of the onset of dawn singing after playback. We calculated the time shift in the onset of dawn singing as the time of singing at the second dawn (second day) minus the time of singing at the first dawn (first day). Because dawn singing by individual males may change as the Spring season progresses, we calculated the adjusted time shift in the onset of dawn singing by comparing the experiment and control groups: the time shift in dawn singing by species in the experimental group minus the time shift in dawn singing by species in the control group. Negative values

indicated a species singing earlier in the second dawn chorus than in the first dawn chorus.

To determine whether dawn chorusing in bird communities is influenced by the Brownish-Flanked Bush Warbler, we used meta-analysis with random effects models (Chen & Peace, 2013) to compare the time shift in the onset of dawn singing between the experimental and control groups. Typically, meta-analysis combines the results of several studies by calculating the weighted mean of the effect size, known as the summary effect (Borenstein et al., 2011). For the meta-analysis, we excluded the Brownish-flanked Bush Warbler records and considered all other species as independent samples (studies). The time shift in the onset of dawn singing was used as the effect size and was weighted by the number of recording sites at which each species was recorded. For the random effects model, we assumed that the true effect size (shift in dawn singing) varied from species to species, with the summary effect being the mean estimate of the distribution of effect sizes. The meta-analysis was performed using the package *meta* (Schwarzer, 2015) in R software, v. 3.3.1 (R Core Development Team, 2016).

To calculate the similarity of the songs of all target species to that of the Brownishflanked Bush Warbler, we first averaged measurements over 15 songs for each species and then used principal component analysis (PCA) with Varimax rotation to generate principal components on the basis of the averaged data. Two principal components had eigenvalues > 1.0, thus explaining 87.9% of the variance in the original 6 variables (Table 1). Euclidean distances based on these two principal components were used as the measurement of song dissimilarity to that of the Brownish-flanked Bush Warbler. We used a linear regression model to test whether song features, niches, and phylogenetic relatedness affect the adjusted time shift in the onset of dawn singing. In the model, each species was considered as an independent sample, with the adjusted time shift in the onset of dawn singing included as the dependent variable and song dissimilarity, niches and phylogenetic distance to the Brownish-flanked Bush Warbler as independent variables. PCA and linear regression models were conducted using R software, v. 3.3.1 (R Core Development Team, 2016).

## Results

The RASC analyses identified a distinctive sequential pattern of dawn singing among the ten species across both mornings. On the first morning, the first species to engage in dawn singing was the Blackbird, followed by the Brownish-flanked Bush Warbler, Spectacled Laughingthrush, Vinous-throated Crowtit and Great Tit (Figure 3). After the playback of the Brownish-flanked Bush Warbler's song on the afternoon of the first day, the RASC sequential ordering of dawn singing for the second day revealed a different pattern, with the Brownish-flanked Bush Warbler singing first, followed by the Blackbird, Vinous-throated Crowtit, Red-headed Tit and Rufous-necked Scimitar Babbler (Figure 3).

Within the experimental group (with playback in the first afternoon), nine out of ten species sang earlier in the second dawn than the first, with time shifts ranging from 84 s to 609 s, with the exception of the Rufous-necked Scimitar Babbler, which sang 165 s later in the second dawn (Figure 4). For the control group (without playback in the first afternoon), 4 species sang earlier in the second dawn chorus, with time shifts ranging from 66 s to 841 s, whereas five species sang later in the second dawn, with time shifts ranging from 82 s to 610 s (Figure 4). With the exception of the Red-headed Tit, which sang earlier in the control group, all other species sang earlier in the experimental group than in the control group (Figure 4).

Meta-analysis revealed that the timing of dawn singing among these species was 251 s earlier on the second day than the first day (random effects meta-analysis model, P = 0.043) (Figure 5). The adjusted time shift of the onset of dawn singing also varied significantly among species (linear model,  $F_{3,6} = 9.40$ , P = 0.011,  $R^2 = 0.91$ ). Species whose song was more similar to the Brownish-flanked Bush Warbler's song sang significantly earlier on the second morning (linear model, coefficient =  $368.22 \pm 129.73$  (mean  $\pm$  SE), t = 2.838, P = 0.030; Figure 6a), and species that were more distantly related to the Brownish-flanked Bush Warbler also sang significantly earlier (linear model, coefficient =  $-22.34 \pm 6.19$ , t = -3.609, P = 0.011; Figure 6b). There is no significant difference in adjusted time shift of the onset of dawn singing between species with and without similar niches to the Brownish-flanked Bush Warbler (linear model, coefficient =  $84.49 \pm 148.43$ , t = -0.569, P = 0.590).

#### Discussion

After the playback of Brownish-flanked Bush Warbler song on a previous day, eight of the nine investigated species shifted the onset of their dawn singing to an earlier time, whereas only one species sang later in the experiment group compared to the control group. Timing of dawn singing shift in each single species is not significant, which may be due to the low statistical power. As a meta-analysis is a more powerful test than each single statistical test (Borenstein et al., 2011), we found a significant trend to singing earlier in the bird community accompanying with increasing dawn singing intensity in the Brownish-flanked Bush Warbler. The onset of dawn singing is influenced by both environmental (e.g. Barnett & Briskie, 2007; Hutchinson, 2002; York et al., 2014) and

biological factors (e.g. Berg et al., 2006; Hamao, 2008; Stehelin & Lein, 2014). Environmental factors (such as sunshine, moonlight, cloudiness) similarly affected experimental and control groups. Biological factors (like eye size, reproductive stage, interactive among conspecifics) vary among species, and we randomly divided recording sites into the experimental group and control group, so it seems unlikely that species with earlier singing in experimental than the control group was due to biological factors. Compared to the control group, we did 15 min playback of Brownish-flanked Bush Warbler song in the afternoon of the first day and found conspecific males increased dawn singing intensity in the second dawn in the experiment group (Xia et al., 2014). We did not find any species, other than Brownish-flanked Bush Warbler, responding (singing and flying to the loud-speaker) to the playback. After ruling out effects of environmental factors, biological factors, and interspecific responses to the playbacks, the temporal shifts in dawn singing in the community in the experimental group is possibly most influenced by increasing dawn singing intensity in the Brownish-flanked Bush Warbler.

Dawn singing by the Brownish-flanked Bush Warbler could influence singing by other species in serval ways. As suggested by Gorissen et al. (2006) and Grava et al. (2012), response toward heterospecific song may due to interspecific competition for resources. However, this hypothesis was not supported in our system, as both species, with or without similar niches to the Brownish-flanked Bush Warbler, sang earlier. Interspecific competition for "transmission channels" during dawn could be another reason for such temporal shifts. Previous research has shown that cicada singing and anthropogenic sounds masking song of certain bird species lead to temporal shifts of singing activity in these species (e.g. Arroyo-Solis et al., 2013; Gil et al., 2015; Hart et al., 2015; Stanley et al., 2016). Although species, whose song was more similar to Brownish-flanked Bush Warbler song, shifted the onset of their dawn singing more, we do not consider that this temporal shift is due to competition for "transmission channels". Unlike the sounds produced by cicadas and traffic noise, which are somewhat continuous and occur at high volume, Brownish-flanked Bush Warblers sing approximately 4 songs per min during dawn (Xia et al., 2014), and each song lasts approximately 2.5 s (Xia et al., 2013), so it is unlikely to mask other species singing. Møller (1992) suggested that bird song can act as a cue of predator absence. Brownish-flanked Bush Warblers sang earlier in the dawn after simulated territorial insertions the previous afternoon. Other sympatric songbird species may use this earlier singing as interspecific social information about predator absence, and increase their singing activity. Thus, we found a significant trend to singing earlier in the bird community accompanied by an increase in the dawn singing intensity in the Brownish-flanked Bush Warbler. However, there is also another possibility. Only some species were influenced by earlier singing of Brownish-flanked

Bush Warbler, which then subsequently influenced singing of other species. Considering the small sample sizes for each species (range from 6 to 19), we could not identify which species was directly or indirectly influenced by Brownish-flanked Bush Warbler.

Previous research regarding heterospecific song influence has largely focused on closely related species, particularly congeners. For example, Banded Wrens (*Thryophilus pleurostictus*) are known to respond strongly to both conspecific and congeneric Rufous-and-white Wrens (*Thryophilus rufalbus*) song playback (Hick et al., 2015; Hick et al., 2016); Thrush Nightingale (*Luscinia luscinia*) shows similar significant responses to the playback of both Common Nightingale (*Luscinia megarhynchos*) and Thrush Nightingale songs (Reif et al., 2015). Our study is one of few showing how bird song influences heterospecific singing even in different taxonomic families. Further, we found that species that were more distantly related to Brownish-flanked Bush Warbler shifted the onset of their dawn singing the most. If the influence of heterospecific singing on the onset of dawn chorus is a general phenomenon amongst passerines, this may influence the temporal organization of song activity in the community, and result in synchronization in singing activities among different species, such as singing in dawn and dusk chorus (Møller, 1992).

## References

- Agterberg, F. P., & Gradstein, F. M. (1999). The RASC method for ranking and scaling of biostratigraphic events. Earth-Science Reviews 46, 1–25. doi: 10.1016/S0012-8252(99)00007-0
- Arroyo-Solis, A., Castillo, J. M., Figueroa, E., Lopez-Sanchez, J. L., & Slabbekoorn, H. (2013). Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban birds. Journal of Avian Biology 44, 288-296. doi: 10.1111/j.1600-048X.2012.05796.x
- Barnett, C. A., & Briskie, J. V. (2007). Energetic state and the performance of dawn chorus in silvereyes (*Zosterops lateralis*). Behavioral Ecology and Sociobiology 61, 579-587. doi: 10.1007/s00265-006-0286-x
- Berg, K. S., Brumfield, R. T., & Apanius, V. (2006). Phylogenetic and ecological determinants of the neotropical dawn chorus. Proceedings of the Royal Society B: Biological Sciences 273, 999-1005. doi: 10.1098/rspb.2005.3410
- Borenstein, M., Hedges, L. V., Higgins, J. P., & Rothstein, H. R. (2011). Introduction to meta-analysis. West Sussex: John Wiley & Sons.
- Brouwer, L., van de Pol, M., Aranzamendi, N. H., et al. (2017). Multiple hypotheses explain variation in extra-pair paternity at different levels in a single bird family. Molecular Ecology 26, 6717-6729. doi: 10.1111/mec.14385
- Burt, J. M., & Vehrencamp, S. L. (2005). Dawn chorus as an interactive communication network. In McGregor, P. K. (Eds), Animal communication networks (pp. 320-

343). New York: Cambridge university press.

- Chen, D.-G. D., & Peace, K. E. (2013). Applied meta-analysis with R. Boca Raton: CRC Press.
- DeJong, L. N., Cowell, S. D., Nguyen, T. N. N., & Proppe, D. S. (2015). Attracting songbirds with conspecific playback: a community approach. Behavioral Ecology 26, 1379-1388. doi: 10.1093/beheco/arv094
- Fallow, P. M., Gardner, J. L., & Magrath, R. D. (2011). Sound familiar? Acoustic similarity provokes responses to unfamiliar heterospecific alarm calls. Behavioral Ecology 22, 401-410. doi: 10.1093/beheco/arq221
- Fallow, P. M., Pitcher, B. J., & Magrath, R. D. (2013). Alarming features: birds use specific acoustic properties to identify heterospecific alarm calls. Proceedings of the Royal Society B: Biological Sciences 280, 20122539. doi: 10.1098/rspb.2012.2539
- Foote, J. R., Fitzsimmons, L. P., Mennill, D. J., & Ratcliffe, L. M. (2010). Black-capped chickadee dawn choruses are interactive communication networks. Behaviour 147, 1219-1248. doi: 10.1163/000579510X513761
- Foote, J. R., Fitzsimmons, L. P., Mennill, D. J., & Ratcliffe, L. M. (2011). Male blackcapped chickadees begin dawn chorusing earlier in response to simulated territorial insertions. Animal Behaviour 81, 871-887. doi: 10.1016/j.anbehav.2011.01.028
- Gil, D., Honarmand, M., Pascual, J., Pérez-Mena, E., & Garcia, C. M. (2015). Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. Behavioral Ecology 26, 435–443. doi: 10.1093/beheco/aru207
- Gorissen, L., Gorissen, M., & Eens, M. (2006). Heterospecific song matching in two closely related songbirds (*Parus major* and *P. caeruleus*): great tits match blue tits but not vice versa. Behavioral Ecology and Sociobiology 60, 260-269. doi: 10.1007/s00265-006-0164-6
- Grava, A., Grava, T., & Otter, K. A. (2012). Differential response to interspecific and intraspecific signals amongst chickadees. Ethology 118, 711-720. doi: 10.1111/j.1439-0310.2012.02061.x
- Haff, T. M., & Magrath, R. D. (2013). Eavesdropping on the neighbours: fledglings learn to respond to heterospecific alarm calls. Animal Behaviour 85, 411-418. doi: 10.1016/j.anbehav.2012.11.016
- Hamao, S. (2008). Singing strategies among male black-browed reed warblers *Acrocephalus bistrigiceps* during the post-fertile period of their mates. Ibis 150, 388–394. doi: 10.1111/j.1474-919X.2008.00803.x
- Hammer, Ø., Harper, D. A., & Ryan, P. D. (2001). PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4, 1-9.
- Hart, P. J., Hall, R., Ray, W., Beck, A., & Zook, J. (2015). Cicadas impact bird communication in a noisy tropical rainforest. Behavioral Ecology 26, 839-842. doi: 10.1093/beheco/arv018
- Hick, K. G., Doucet, S. M., & Mennill, D. J. (2015). Interspecific vocal discrimination in Neotropical wrens: responses to congeneric signals in sympatry and allopatry.

Animal Behaviour 109, 113-121. doi: 10.1016/j.anbehav.2015.08.008

- Hick, K. G., Doucet, S. M., & Mennill, D. J. (2016). Tropical wrens rely more on acoustic signals than visual signals for inter- and intraspecific discrimination. Animal Behaviour 118, 153-163. doi: 10.1016/j.anbehav.2016.05.024
- Hutchinson, J. M. C. (2002). Two explanations of the dawn chorus compared: how monotonically changing light levels favour a short break from singing. Animal Behaviour 64, 527-539. doi: 10.1006/anbe.2002.3091
- Jetz, W., Thomas, G., Joy, J., Hartmann, K., & Mooers, A. (2012). The global diversity of birds in space and time. Nature 491, 444-448. doi: 10.1038/nature11631
- Kivela, S. M., Seppanen, J.-T., Ovaskainen, O., Doligez, B., Gustafsson, L., Monkkonen, M., & Forsman, J. T. (2014). The past and the present in decisionmaking: the use of conspecific and heterospecific cues in nest site selection. Ecology 95, 3428-3439. doi: 10.1890/13-2103.1
- Kroodsma, D. E., & Byers, B. E. (1991). The function (s) of bird song. American Zoologist 31, 318-328. doi: 10.1093/icb/31.2.318
- Li, J. Q., Lv, L., Wang, Y., Xi, B., & Zhang, Z. W. (2012). Breeding biology of two sympatric *Aegithalos* tits with helpers at the nest. Journal of Ornithology 153, 273-283. doi: 10.1007/s10336-011-0740-z
- Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. Biological Reviews 90, 560-586. doi: 10.1111/brv.12122
- Martin, P. R., & Martin, T. E. (2001). Behavioral interactions between coexisting species: song playback experiments with wood warblers. Ecology 82, 207-218. doi: 10.1890/0012-9658(2001)082%5B0207:BIBCSS%5D2.0.CO;2
- Medina, I., Langmore, N. E., Lanfear, R., et al. (2017). The evolution of clutch size in hosts of avian brood parasites. American Naturalist 190, E112-E123. doi: 10.1086/693778
- Møller, A. P. (1992). Interspecific response to playback of bird song. Ethology 90, 315-320. doi: 10.1111/j.1439-0310.1992.tb00842.x
- Munoz, N. E., Brandstetter, G., Esgro, L., Greene, W., & Blumstein, D. T. (2015). Asymmetric eavesdropping between common mynas and red-vented bulbuls. Behavioral Ecology 26, 689-696. doi: 10.1093/beheco/aru206
- Olalla-Tarraga, M. A., Gonzalez-Suarez, M., Bernardo-Madrid, R., et al. (2017). Contrasting evidence of phylogenetic trophic niche conservatism in mammals worldwide. Journal of Biogeography 44, 99-110. doi: 10.1111/jbi.12823
- Poesel, A., Kunc, H. P., Foerster, K., Johnsen, A., & Kempenaers, B. (2006). Early birds are sexy: male age, dawn song and extrapair paternity in blue tits, *Cyanistes* (formerly *Parus*) *caeruleus*. Animal Behaviour 72, 531-538. doi: 10.1016/j.anbehav.2005.10.022
- Reif, J., Jiran, M., Reifova, R., Vokurkova, J., Dolata, P. T., Petrusek, A., & Petruskova, T. (2015). Interspecific territoriality in two songbird species: potential role of song convergence in male aggressive interactions. Animal Behaviour 104, 131-136. doi: 10.1016/j.anbehav.2015.03.016
- Schepers, M. J., & Proppe, D. S. (2016). Song playback increases songbird density near

low to moderate use roads. Behavioral Ecology 28, 123-130. doi: 10.1093/beheco/arw139

- Schmidt, K. A., & Belinsky, K. L. (2013). Voices in the dark: predation risk by owls influences dusk singing in a diurnal passerine. Behavioral Ecology and Sociobiology 67, 1837-1843. doi: 10.1007/s00265-013-1593-7
- Schwarzer, G. (2015). meta: General Package for Meta-Analysis. Retrieved from http://CRAN.R-project.org/package=meta
- Seppanen, J-T., & Forsman, J. T. (2007). Interspecific social learning: Novel preference can be acquired from a competing species. Current Biology 17, 1248-1252. doi: 10.1016/j.cub.2007.06.034
- Seppanen, J-T., Forsman, J. T., Monkkonen, M., Krams, I., & Salmi, T. (2011). New behavioural trait adopted or rejected by observing heterospecific tutor fitness. Proceedings of the Royal Society B-Biological Sciences 278, 1736-1741. doi: 10.1098/rspb.2010.1610
- Silva, A. D., Samplonius, J. M., Schlicht, E., Valcu, M., & Kempenaers, B. (2014). Artificial night lighting rather than traffic noise affects the daily timing of dawn and dusk singing in common European songbirds. Behavioral Ecology 25, 1037-1047. doi: 10.1093/beheco/aru103
- Silva, A. D., Valcu, M., & Kempenaers, B. (2016). Behavioural plasticity in the onset of dawn song under intermittent experimental night lighting. Animal Behaviour 117, 155-165. doi: 10.1016/j.anbehav.2016.05.001
- Slater, P. J. B. (2003). Fifty years of bird song research: a case study in animal behaviour. Animal Behaviour 65, 633-639. doi: 10.1006/anbe.2003.2051
- Soberon, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters 10, 1115-1123. doi: 10.1111/j.1461-0248.2007.01107.x
- Staicer, C. A., Spector, D. A., & Horn, A. G. (1996). The dawn chorus and other diel patterns in acoustic signaling. In Kroodsma, D. E., & Miller, E. H. (Eds) Ecology and evolution of acoustic communication in birds (pp. 426-453). New York: Cornell university press.
- Stanley, C. Q., Walter, M. H., Venkatraman, M. X., & Wilkinson, G. S. (2016). Insect noise avoidance in the dawn chorus of Neotropical birds. Animal Behaviour 112, 255-265. doi: 10.1016/j.anbehav.2015.12.003
- Stehelin, T. E., & Lein, M. R. (2014). Social stimulation of dawn singing in Dusky Flycatchers: a serendipitous experiment. Journal of Field Ornithology 85, 63-74. doi: 10.1111/jofo.12050
- Thomas, R. J., Szekely, T., Cuthill, I. C., Harper, D. G. C., Newson, S. E., Frayling, T. D., & Wallis, P. D. (2002). Eye size in birds and the timing of song at dawn.
  Proceedings of the Royal Society of London Series B: Biological Sciences 269, 831-837. doi: 10.1098/rspb.2001.1941
- Wilman, H., Belmaker, J., Simpson, J., et al. (2016). EltonTraits 1.0: Species level foraging attributes of the world's birds and mammals. Ecology 95, 2027-2027. doi: 10.1890/13-1917.1
- Xia, C. W., Lin, X. L., Liu, W., Lloyd, H., & Zhang, Y. Y. (2012). Acoustic identification

of individuals within large avian populations: a case study of the Brownishflanked Bush Warbler, South-Central China. PLoS One 7, e42528. doi: 10.1371/journal.pone.0042528

- Xia, C. W., Liu, J. Y., Alström, P., Wu, Q., & Zhang, Y. Y. (2013). Is the soft song of the brownish-flanked bush warbler an aggressive signal? Ethology 119, 653-661. doi: 10.1111/eth.12104
- Xia, C. W., Wei, C. T., Lloyd, H., Liu, J. Y., Wu, Q., & Zhang, Y. Y. (2014). Dawn singing intensity of the male brownish-flanked bush warbler: effects of territorial insertions and number of neighbors. Ethology 120, 324-330. doi: 10.1111/eth.12205
- York, J. E., Young, A. J., & Radford, A. N. (2014). Singing in the moonlight: dawn song performance of a diurnal bird varies with lunar phase. Biology Letters 10, 20130970. doi: 10.1098/rsbl.2013.0970

Species	Maximum frequency	Minimum frequency	Peak frequency	Duration	Number of	Number	PC1	PC2	Song
	(kHz)	(kHz)	(kHz)	(s)	notes	different notes			dissimilarity
Yellow-bellied Tit	$8.44\pm0.27$	3.88 ± 0.11	$5.39 \pm 0.31$	$0.96 \pm$	$5.67\pm0.85$	$2.20 \pm 0.11$	1.11	-0.27	1.53
				0.09					1.00
Great Tit	$8.28\pm0.08$	$3.14 \pm 0.16$	$5.32 \pm 0.25$	$0.65 \pm$	$4.20 \pm 0.45$	$2.47 \pm 0.22$	0.80	-0.48	1.33
				0.06					
Rufous-necked Scimitar-	$2.72 \pm 0.21$	$1.63 \pm 0.08$	$2.19 \pm 0.16$	$0.69 \pm$	$3.67\pm0.42$	$2.00 \pm 0.00$	-1.08	-0.87	1.28
Babbler	$2.72 \pm 0.21$	1.05 ± 0.00	$2.17 \pm 0.10$	0.06					
Spectacled Laughingthrush	$2.96 \pm 0.04$	$1.10 \pm 0.03$	$2.53 \pm 0.04$	$0.16 \pm$	$2.00 \pm 0.24$	$1.33 \pm 0.13$	-1.18	-1.29	1.69
				0.01					
Hwamei	$4.01 \pm 0.13$	$1.44 \pm 0.06$	$2.68 \pm 0.13$	$4.59 \pm$	15.93 ± 1.89	$5.07 \pm 0.32$	-0.42	2.08	1.89
				0.57					
Vinous-throated Crowtit	$8.24 \pm 0.49$	2.61 ± 0.28	$4.74 \pm 0.13$	$0.85 \ \pm$	8.47 ± 1.47	$1.00 \pm 0.00$	0.71	-0.21	1.14
				0.12					
Collared Finchbill	$3.60 \pm 0.06$	$1.33 \pm 0.04$	3.12 ± 0.11	$0.97 \pm$	$5.13 \pm 0.27$	$4.07 \pm 0.25$	-0.83	-0.28	0.67
				0.10					
Red-headed Tit	8.62 ± 0.21	$4.37\pm0.42$	$7.12 \pm 0.1$	$0.46 \pm$	8.07 ± 0.69	1.93 ± 0.12	1.70	-0.19	2.09
				0.05					
Brownish-flanked Bush	5.57 ± 0.11	$1.63 \pm 0.06$	$3.75 \pm 0.16$	$2.26 \pm$	4.47 ± 0.19	$4.47 \pm 0.19$	-0.36	0.19	0
Warbler				0.06					
Blackbird	$6.28\pm0.65$	$1.45 \pm 0.05$	$2.28\pm0.07$	$2.30 \pm$	$10.47 \pm 1.76$	$7.60 \pm 1.04$	-0.44	1.33	1.15

Table 1. Song measurements for the 10 species in this study (mean  $\pm$  SE, calculated from 15 songs in each species). Song dissimilarity is presented as the Euclidean distance between the two principal components.

0.23

Figure Legends:

Figure 1. Phylogenetic tree of the 10 species in this study. Phylogenetic data were obtained from Jetz et al. (2012).

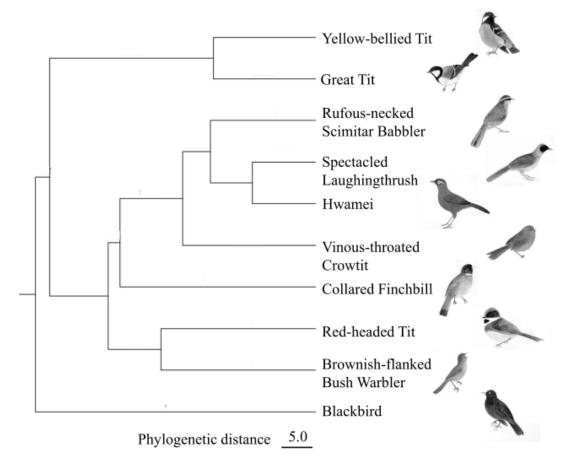


Figure 2. Spectrograms of the songs representing the ten species in the study.

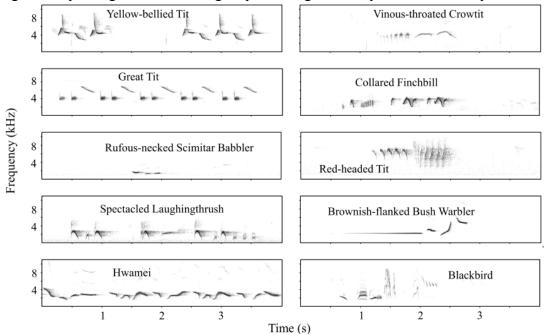


Figure 3. The sequential order of the start of dawn singing before playback (first dawn) and after playback (second dawn) of all ten species identified using ranking-scaling analyses.

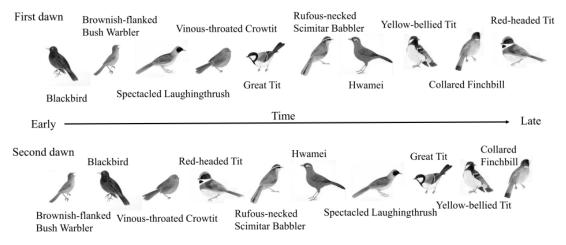


Figure 4. Shifts in the time of dawn singing (the singing time on the second day minus the singing time on the first day) for each species (mean ± standard deviation). Negative values indicate species singing earlier on the second day. Black bars represent the experimental group (with playback in the first afternoon); open bars represent the control group (without playback in the first afternoon). A: Yellow-bellied Tit; B: Great Tit; C: Rufous-necked Scimitar-Babbler; D: Spectacled Laughingthrush; E: Hwamei; F: Vinous-throated Crowtit; G: Collared Finchbill; H: Red-headed Tit; I: Blackbird.

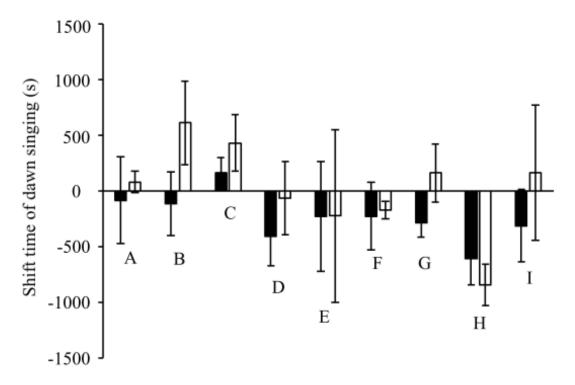


Figure 5. Temporal shifts of dawn singing by the nine species.

There is no significant difference in time shift of dawn signing between before and after playback in single species (95% confidence intervals overlap 0 in all species), but the whole community sing early on the second day after playback (95% confidence interval is less than 0). Effect sizes of the bird community were calculated using a random effects meta-analysis model. Horizontal lines represent the effect size with 95% confidence intervals for each species, and blocks indicate the weight of each species in the meta-analysis. The diamond indicates the summary effect with 95% confidence intervals, and the dotted line represents the mean summary effect. Negative values along the x-axis indicate species with an earlier onset of dawn singing on the second day after playback.

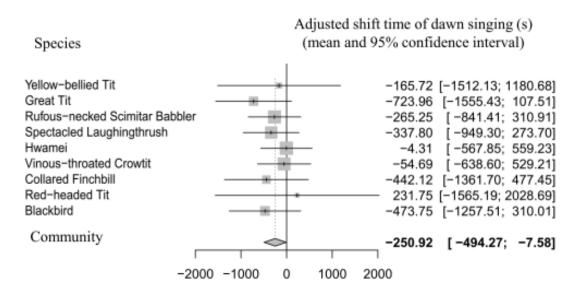


Figure 6. (a) Similarity in the songs of nine species to the song of the Brownish-flanked Bush Warbler, and (b) phylogenetic distance of the nine species to the Brownishflanked Bush Warbler, with adjusted time shift in the onset of dawn singing. Phylogenetic data were obtained from Jetz et al. (2012). Negative values on the y-axis indicate species singing earlier on the second day than the first day. A: Yellow-bellied Tit; B: Great Tit; C: Rufous-necked Scimitar-Babbler; D: Spectacled Laughingthrush; E: Hwamei; F: Vinous-throated Crowtit; G: Collared Finchbill; H: Red-headed Tit; I: Blackbird.

