Insect noise avoidance in the dawn chorus of Neotropical birds
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Many species of birds conspicuously call or sing early in the morning, thereby creating an avian dawn chorus. While these vocalizations probably function to advertise territory occupancy, when species should start singing is not well understood. A common explanation is that birds sing at dawn to maximize signal transmission due to low atmospheric turbulence during the early morning (acoustic transmission hypothesis); however, this idea does not explain why species in the chorus often start singing at different times. Here we test a version of this hypothesis: interspecific differences in call start times during the dawn chorus are a result of noise avoidance at the song’s frequency. To test this hypothesis we quantified the spectral and temporal properties of the dawn chorus and the acoustic landscape at Barro Colorado Island, Panama. Inspection of 36 dawn recordings at 12 sites identified 27 species of birds, with most species having consistent start times across sites and days. In contrast to expectations, we found that birds singing within the same frequency range did not temporally partition acoustic space during the chorus. Discriminant function analysis revealed that nearly all species in the chorus produced distinctive vocalizations. Surprisingly, song start time was positively related to peak frequency. Birds with high-frequency vocalizations did not begin singing until after orthopteran insects stopped producing loud sounds at the same frequencies. These results suggest that birds that sing at frequency bands shared by nocturnal insects avoid acoustic masking by delaying song start times. Playbacks of emerald cicada, Zammara smaragdina, buzzes conducted during the dawn chorus produced an inhibitory effect on the call activity of birds singing within the bandwidth of cicada calls. Thus, insect noise appears to create an important frequency-dependent constraint on the calling activity of birds. This constraint is overcome by temporal partitioning of acoustic space.

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The dawn chorus occurs during a short period of the morning when most members of the avian community call or sing together. This daily occurrence is so regular that numerous species have been reported to begin singing at characteristic times every morning (Allard, 1930; Leopold & Eynon, 1961). Although often pleasing to the human ear, this cacophony creates a dilemma for all participants: when should an individual sing in order to be heard most clearly? Given the important role that song plays in both territory defence and mate acquisition for birds, being heard by conspecifics should have direct fitness advantages, leading to selection for mechanisms to ensure detection and discrimination of individuals (Endler, 1992; Wiley, 2006). Consequently, species-specific signals that are sufficiently different in spectral or temporal features to avoid interference and signal masking within the acoustic community are expected to evolve (Endler, 1993; Wiley, 2006). In addition to avoiding heterospecific interference, birds must also compete for acoustic space from other sources of noise (e.g., wind, insect, anthropogenic; Brumm & Slabbekoorn, 2005). This can be particularly challenging in some habitats, such as tropical rainforests, where dense vegetation interferes with long-distance signalling and species from a variety of taxa produce sounds (Luther, 2009; Ryan & Brenowitz, 1985; Slabbekoorn, 2004). This combination of high acoustic diversity and restricted calling period provides an excellent setting in which to examine the mechanisms used by animals to increase the overall active space of their signal and ensure effective communication. Ambient noise has long been considered an important constraint on avian acoustic signal design (Brenowitz, 1982; Brumm & Slabbekoorn, 2005; Ryan & Brenowitz, 1985; Wiley, 1994, 2006). Heterospecific birdsong can be a common source of acoustic...
interference, and evidence of acoustic space partitioning has been found in Neotropical avian assemblages (Luther, 2009; Planqué & Slabbekoorn, 2008). In addition, nonavian noise can have an equally important influence on the transmission and reception of avian acoustic signals. In particular, some bird species adjust both the spectral and temporal properties of their songs to minimize overlap with anthropogenic noise in urban environments (e.g. Brumm, 2004; Fuller, Warren, & Gaston, 2007; Wood & Yeyerinac, 2006). Tropical forests are another habitat with high background noise that can be heterogeneous in space, time and frequency, creating a complex acoustic landscape in which animals have to communicate (Luther & Gentry, 2013; Rodriguez et al., 2014). Many tropical animals use sound for communication, including various insects, such as orthopterans (crickets and katydids) and hemipterans (cicadas), as well as various nonavian vertebrates including frogs and mammals. Many insect sounds are loud, exhibit frequency overlap with some bird sounds and vary temporally with a peak at night and cessation at sunrise (Diwakar & Balakrishnan, 2007; Lang, Teppner, Hartbauer, & Römer, 2005). Such nonavian noise has considerable potential to interfere with avian communication at dawn but has received comparatively little study.

How selection operates on the timing of acoustic signals and particularly why dawn chorus is such a widely employed strategy of communication remain open questions. Three nonmutually exclusive hypotheses have been proposed to describe why birds sing at dawn. The acoustic transmission hypothesis posits that dawn is the best time of day for the propagation and discrimination of acoustic signals due to favourable temperature, humidity and wind (Brenowitz, 1982; Brown & Handford, 2003; Henwood & Fabrick, 1979). The energy storage stochasticity hypothesis predicts that the optimal time for a bird to sing is at dawn (and dusk) in order to take advantage of energy reserves remaining from the previous night (owing to unpredictable overnight energy requirements; Hutchinson, 2002; McNamara, Mace, & Houston, 1987). The inefficient foraging hypothesis links the timing of dawn chorus to light availability (Berg, Brumfield, & Apanius, 2006; Thomas et al., 2002) and predicts that dawn choruses occur in the interim low-light period between when birds are first able to initiate territorial advertisements and when they are able to forage effectively (Armstrong, 1963; Kacelnik, 1979; Krans, 2001). The inefficient foraging hypothesis is the only hypothesis that has been used to address the staggered start time of different species during a dawn chorus, linking eye size (a measure of a species’ ability to see in low light) to song start time (Berg et al., 2006; Thomas et al., 2002). At a community level, the acoustic transmission hypothesis has found support explaining the timing of the dawn chorus, since low air turbulence at dawn maximizes sound propagation and detectability (Brown & Handford, 2003; Henwood & Fabrick, 1979). It has not, by contrast, been used to explain interspecific differences in song start times, as atmospheric conditions are expected to be similar for most, if not all, species in an assemblage. However, other factors, such as ambient noise, do vary across time and frequency and could potentially result in species-specific periods when the active space of a call is maximal.

In this paper we examine when birds join the dawn chorus in a Neotropical rainforest. In particular we investigate an expanded version of the acoustic transmission hypothesis to determine whether ambient noise that has the potential to reduce signal detection and discrimination could explain interspecific differences in song start times during the dawn chorus. We evaluate whether different bird species disperse their calls or songs in acoustic space to avoid spectral or temporal overlap with each other or with other noise in the environment. We predicted that birds join a chorus at different times to avoid temporal overlap with both avian and nonavian noise at their song frequency. We also experimentally assessed whether some species of birds avoid nonavian noise by altering their singing behaviour. Cicadas produce long, broadband signals that dominate the acoustic background in tropical lowland forests during the day (Nischk & Riede, 2001). By simulating cicada noise using playbacks, we tested whether birds actively avoid insect noise when it occurs at their song frequency through an immediate change in singing activity.

METHODS

Ethical Note

This study was approved by the University of Maryland Institutional Animal Care and Use Committee (579030-1) and by the Smithsonian Tropical Research Institute (2014-0815-2017).

Study Site and Recording Methods

Audio recordings of the dawn chorus were made over a 2-week period during the wet season (late August, 2014) on Barro Colorado Island (BCI), Panama (9°09’N, 79°51’W). BCI is a 1562 ha land-bridge island located in Gatun Lake within the Panama Canal. The island has been isolated from the mainland since the Panama Canal was formed in 1911 and consists of secondary forest with areas of less disturbed old growth forest (Willis, 1974). Average annual precipitation at BCI is approximately 2960 mm, and the life zone is characterized as tropical moist forest (Holdridge, 1967). We conducted a total of 36 hour-long recordings at 12 sites located in secondary forest on the eastern half of the island, at least 300 m from occupied buildings (Supplementary Fig. S1). We visited each site twice within a 2-week period to record ambient sounds at dawn with a single recording unit. In addition, we visited six of these sites with two recording units to monitor responses to cicada playbacks as described below. We started 30 min before nautical twilight and recorded for 1 h to capture the first calls of birds joining the dawn chorus. Recordings were not made in the rain.

We used four ZOOM H2n Handy Recorders (Tokyo, Japan) connected to Sennheiser ME 66 microphones with a flat frequency response between 200 and 6000 Hz (±2 dB) to make recordings. During each recording period we continuously monitored sound levels and pointed microphones towards vocalizing birds. The Sennheiser ME 66 is directional in that sounds within 30° of where the microphone is aimed are recorded ±2 dB while sounds 90° or greater away are reduced by 10 dB or more. Consequently, the directional sensitivity of the microphones allowed us to identify species from distant calls despite background noise and generate high-quality spectrograms for species identification and acoustic measurements. Files were digitized at 16 bits with a sampling frequency of at least 44.1 kHz and saved in WAV format. On day 1, we manually adjusted the input gain while recording. On day 2 and onwards we set the input gain of the four recording units to the maximum, which significantly improved the maximum range of each recording unit. Therefore, the files obtained from the first day were used only for call identification and not for quantifying relative changes of background noise during the dawn chorus. We did not attempt to measure absolute amplitude values of ambient noise. Reported noise values are, therefore, relative to the maximum input amplitude of the microphone—recorder combination (ca. 120 dB).

Call and Noise Measurements

We counted calls by listening to recordings and analysing spectrograms created by Raven Pro v.1.4 (http://www.birds.cornell.edu/rbr/raven/ravenversions) using a Hann window, FFT = 4096 and
We identified the species of bird that produced each call by comparing sounds and spectrograms to recordings available from Xeno-Canto (www.xeno-canto.org) and the Macaulay Library (Cornell University, Ithaca, NY, U.S.A.) and then created a library of audio and spectrogram samples for each species. Species identifications (see Appendix, Table A1) were confirmed by expert field guides that were conducting point counts on BCI. For each recording session we counted the number of discrete calls recorded for each species in each 5 min time period or for species with continuous calls, such as crested guan, Penelope purpurascens, and mealy amazon parrot, Amazona farinosa, we counted the number of seconds in which calls occurred. We also noted the time at which the first call of each species occurred for every recording session. While some nocturnal species, such as owls, were identified in the recordings, only diurnal species are included in our analyses.

To quantify acoustic features of calls and background noise, we used Selena, a custom-made sound analysis program developed at the University of Tübingen (Tübingen, Germany). For each species we selected at least three (mean \( SE = 17.7 \pm 2.4 \)) calls with high signal-to-noise ratio for analysis. We used calls from different recording sites and units whenever possible to capture interindividual differences in call features. Using Selena we computed spectrograms (Blackman window, FFT = 2048, variable overlap) with a dynamic range of 80 dB and extracted or calculated the following acoustic features from each call: (1) duration (ms), (2) minimum, (3) maximum frequency, (4) peak frequency (the frequency in Hz with the highest amplitude in the power spectrum), (5) bandwidth (maximum minus minimum frequency), (6) number of notes, (7) complexity (bandwidth divided by duration) and (8) note rate (number of notes divided by duration). Number of notes was manually counted by inspection of the spectrogram. Measurements of complexity and note rate follow Luther (2009). We used the harmonic of the call with the most energy for all measurements. For species that produced multiple types of vocalizations (e.g. cocoa woodcreeper, Xiphorhynchus susurrans), we only used the most common call type for analysis. We analysed a total of 477 calls (see Supplementary Table S1 for summaries of call feature measurements).

We investigated the change in nonavian noise level over the course of the morning by splitting each 1 h recording into 12 equal 5 min bins. Each bin was visualized in Selena as a spectrogram (Blackman window, FFT = 512, 14.2% overlap) with a dynamic range of 90 dB. To quantify nonavian noise, we chose a 5 s interval lacking bird calls, when possible, approximately in the middle of each bin and calculated a mean power spectrum. We then used Selena to calculate the mean noise amplitude across all frequencies in discrete steps. The size of each frequency step is half the sampling number of calls that were classified correctly.

We determined factors that predicted the time at which each species of bird began to sing by fitting a series of linear models using the following five factors as possible explanatory variables: (1) peak frequency of the song, (2) noise avoidance at frequency and time of first song relative to the entire morning, (3) singing location (scored as in canopy or below canopy), (4) diet (scored as insectivorous or other) and (5) body mass (see Supplementary Table S2 for summary of species characteristics). Noise avoidance was calculated for each species by subtracting nonavian noise (as described above) at the time and frequency bin that contained their first call from the average noise (calculated over all other time bins at that frequency step). Given that the goal of the analysis was to determine whether birds actively avoid noise that would mask their songs, we chose the frequency step that included the species’ peak frequency for this analysis as an approximation of masking potential. The maximum deviation between the frequency step used and the actual peak frequency was 21 Hz. All results are reported as the mean over all days and sites unless stated otherwise.
We included singing location to determine whether birds foraging in the canopy sing earlier because there is more light (inefficient foraging hypothesis) and we included diet because birds feeding primarily on animals or fruits would require different light levels for feeding to be profitable (inefficient foraging hypothesis). Body mass was included because larger birds are expected to be more resistant to fasting overnight, leaving more energy reserves in the morning to sing prior to feeding (energy storage stochasticity hypothesis). Information on body mass, location and diet were obtained from Stiles, Skutch, and Gardner (1989). We weighted species by the number of sites where each species was recorded to reflect the amount of information that contributed to each value. We then considered all possible models with main effects or two-way interactions and used Akaike's Information Criterion (corrected for small samples, AICc) to identify the best-fitting model.

To assess the effect of cicada playbacks on singing activity, we conducted two different analyses. First, songs of seven commonly recorded species were counted 1 min before, 1 min during and 1 min after each cicada playback. We then compared the number of songs counted during a playback to those counted after the playback, both expressed as deviations from the number counted before the playback, for each species using paired \( t \) tests. Second, total songs (or seconds of songs) were tallied for each bird at each site on days when cicada playbacks were and were not conducted. Then, we performed a mixed model ANOVA using total song counts from days on which playbacks were performed and treating date as a random effect and playback as a fixed effect for each species of bird that was recorded. We used a sequential Bonferroni correction to adjust alpha for multiple testing.

Unless stated otherwise, all statistical analyses were conducted using JMP v.10.0.2 (SAS Institute, Cary, NC, U.S.A.).

RESULTS

Song Patterns During the Dawn Chorus

Inspection of the average number of singing events counted per site and 5 min interval revealed that the recording sessions successfully captured the peak of the dawn chorus. The average number of singing events increased until 12.5 min after sunrise, when number of singing events reached a maximum before declining (Fig. 2a). In total we counted 76 508 vocalizations from 27 species in 15 families and nine orders (see Appendix Table A1 for common and scientific names, as well as the four-letter code for each species). The number of species recorded at any one site varied from 17 to 25, 11 species were recorded at all 12 sites, and each species was recorded on at least 3 days (Supplementary Table S3). Average time of first song was very consistent for most species across sites and days, with collared forest-falcons, Micrastur semitorquatus, invariably singing first 25 min before dawn, and red-capped manakins, Ceratopipra mentalis, not singing until 15 min after dawn (Fig. 2b). First call time was, therefore, reliably measured by these data.

No significant correlation was found between the absolute difference in peak frequency and the absolute difference in average call activity (Mantel: \( r = 0.141, P = 0.094; \) Supplementary Fig. S3). In fact, the trend was positive, suggesting that species with songs of similar frequency tended to sing at similar times rather than at different times. A discriminant function analysis correctly classified 99.4% of 477 calls to species on the basis of three spectrotemporal features (Fig. 3). All three misclassifications involved white-flanked antwren, Myrmotherula axillaris, and blue-black grosbeak, Cyanocompsa cyanoides. The three discriminant functions accounted for 70.8%, 18.0% and 11.1% of the variation, respectively. The first discriminant function (DF1) was weighted primarily by peak frequency while DF2 and DF3 were influenced primarily by bandwidth/duration and notes/duration (Table 1). Thus, most species did not overlap in peak frequency, but those that did overlap differed sufficiently in song rate or complexity to remain distinctive even when they called simultaneously during a dawn chorus.

Nonavian Noise During the Dawn Chorus

During the dawn chorus, nonavian noise was consistent across sites but highly variable over time. We observed pronounced changes in several distinct frequency bands where noise was high early in the morning and then gradually decreased over time.

Figure 1. Typical spectrogram (FFT = 4096) of a recording made at dawn. Letters indicate (A) a cicada playback and songs of (B) white-flanked antwren, (C) great tinamou, Tinamus major, (D) chestnut-backed antbird, (E) western slaty antshrike and (F) cocoa woodcreeper. Bands of nonavian insect noise are visible between 4 and 8 kHz.
(Fig. 4). These noise bands peaked at 3840 Hz, 6084 Hz and 7465 Hz. Given that the third band fell above the frequency range of birdsong, we did not consider it further. The mean background noise amplitude at the other two peaks decreased by 20.1 dB and 22.5 dB, respectively, across the 1 h sampling period. Background noise amplitudes of frequencies adjacent to these main peaks (3495–4271 Hz and 5739–6472 Hz) also decreased over the 1 h recording period by more than 8 dB. In contrast, nonavian noise was on average 2.8 dB higher at the end of the recording for all frequencies below 3 kHz. Because we could not always find a 5 s window in each 5 min bin without any bird vocalizations, the presence of bird sounds in later bins could explain why the overall amplitude of lower-frequency sounds increased over time. Twenty of the 27 birds had vocalizations with peak frequencies below 3 kHz.

The seven species with songs above 3 kHz experienced a pronounced temporal change in background noise during the dawn period and this was especially true of four species whose peak frequencies fell into one of the two aforementioned noise bands. These species had the lowest noise difference value of all species when noise at first call time was compared to the average noise over the entire morning. These four species were the spotted antbird, Hylophylax naevioides, dot-winged antwren, Microrhopias quixensis, and black-cheeked woodpecker, Melanerpes pucherani, in the first band (peak at 3840 Hz) and the red-capped manakin in the second band (peak at 6084 Hz).

**What Predicts Time of First Call?**

First call time was predicted best by a model that included peak frequency, background noise difference, singing location, and an interaction between singing location and noise difference (Table 2). The over all model fit was highly significant (GLM: $F_{4,22} = 23.04$, $P < 0.0001$, $R^2 = 0.807$, AICc = 234). The next best model had an AICc that was larger by 2.6 (see Supplementary Table S4 for rankings of the top 10 models) and differed from the best model only by
Figure 3. Centroids with 95% confidence intervals plotted for the first two discriminant functions from a quadratic discriminant function analysis using peak frequency, song complexity and song rate for 477 songs from 27 different bird species (see Appendix, Table A1 for species names).

Table 1
Variance explained and standardized coefficients for discriminant functions using three acoustic variables on 477 songs by 27 avian species

<table>
<thead>
<tr>
<th>Discriminant function</th>
<th>Variance explained</th>
<th>Peak frequency</th>
<th>Bandwidth/duration</th>
<th>Notes/duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>DF1</td>
<td>70.8</td>
<td>1.11</td>
<td>–0.31</td>
<td>0.49</td>
</tr>
<tr>
<td>DF2</td>
<td>18.0</td>
<td>–0.13</td>
<td>0.66</td>
<td>0.62</td>
</tr>
<tr>
<td>DF3</td>
<td>11.1</td>
<td>0.003</td>
<td>0.82</td>
<td>–0.77</td>
</tr>
</tbody>
</table>
inclusion of a nonsignificant interaction term between noise difference and peak frequency. Models that included diet had AICc differences larger than 6 while those including body mass had AICc values larger than 10. Thus, neither diet nor body mass contributed to first call time prediction. The relationships between first call time and each factor in the best model are illustrated in Fig. 5. Birds that produced high-frequency songs started singing later in the morning (Fig. 5a). Although song location by itself was not significant, it was included in the best-fitting model because the interaction between song location and noise difference was significant (Table 2). This interaction was present because birds singing from the canopy exhibited a positive relationship between first call time and noise difference while birds singing below the canopy exhibited a negative relationship between first call time and noise difference (Fig. 5b). Thus, birds singing below the canopy appear to delay the start of their singing to reduce interference by nonavian noise.

Response to Cicada Playbacks

Comparison of the number of songs recorded during a playback to the number counted before the playback revealed a significant difference for three of seven common species. Paired t tests revealed that cocoa woodcreepers (t27 = 2.19, P = 0.037), chestnut-backed antbirds, Myrmeciza exsul (t20 = 3.18, P = 0.003) and white-flanked antwrens (t21 = 3.73, P = 0.001) produced fewer songs during playbacks than before the playbacks (Fig. 6a). In contrast, comparison of the number of songs recorded after a playback to the number counted before the playback revealed no effect for any species (Table 3), which indicates that the playback had no lingering effects. The three species that decreased singing activity during playbacks had songs with peak frequencies in the range covered by the cicada playback (cocoa woodcreeper: 2294 Hz; chestnut-backed antbird: 2561 Hz; white-flanked antwren: 2666 Hz) (Fig. 6b; see also Fig. 1, where all three species and cicada calls are displayed).

In addition, mixed model ANOVA on songs recorded per day per site revealed that cicada playbacks significantly altered the calling activity of collared forest-falcons. At sites and days with playbacks, forest-falcon calling was reduced by 78% compared with sites and days without playbacks (Supplementary Table S5). Singing activity of western slaty antshrikes, Thamnophilus atrinucha, was also reduced, but this effect was not significant after adjusting alpha by the sequential Bonferroni procedure. Calling events per day were not altered by cicada playbacks for any other species (Supplementary Table S5).

DISCUSSION

In this study we used observational and experimental approaches to identify factors that influence temporal patterns in the dawn chorus of a Neotropical bird assemblage. We found that each species in the chorus exhibited distinct start times that were consistent across sites and days. Over all, our results indicate that species call at different times to increase the active space of their vocalizations. Thus, our evidence supports a noise-avoidance version of the acoustic transmission hypothesis. But, rather than avoid other species by calling at different times, we found that birds with high-frequency vocalizations began singing at similar times later in the morning. Unexpectedly, the later start times of the high-frequency species corresponded to periods when high-frequency ambient noise declined and, therefore, allowed these species to increase their signal active space. Playbacks of cicada calling bouts confirmed that those species with songs that overlap in frequency with these insects actively reduced their singing activity during playbacks. In contrast, birds that sang below the frequency range of the cicadas did not change their calling activity during a playback, although one species, the collared forest-falcon, appeared to avoid calling at sites where playbacks were conducted. Together these
results suggest that call start times are timed to minimize interference from ambient noise at matching frequencies, most notably from nocturnal insects.

We found no evidence in support of the other two hypotheses for explaining call start times. The inefficient foraging hypothesis suggests that birds singing higher in the canopy would start singing earlier due to higher light levels. Location of singing birds was found to matter, but not as predicted by this hypothesis. We found that birds singing below the canopy exhibited a negative relationship between first call time and background noise difference, resulting in less interference with frequency-matched noise for birds with later start times. In contrast, canopy-dwelling species showed a positive relationship between call time and noise difference, indicating that canopy species that call early experience less noise interference. We found no influence of body size on the time that each species started to sing, as was predicted by the energy stochasticity hypothesis. We suspect this hypothesis may be more suitable for explaining the timing of the dawn chorus by an individual (with regard to individual condition or weather) than for explaining interspecific differences.

Figure 5. First call time measured as minutes from sunrise plotted against (a) peak frequency of each species and (b) the difference between background noise at first call time and over all average background noise for the 1 h period. Background noise values were calculated at each species’ peak frequency band. Each point represents the mean over all days and sites (±SE) per species. Negative noise values indicate that birds started singing at times when ambient noise level at their songs’ peak frequency was lower than the rest of the recording period. Singing location is displayed as either in the canopy (circles, solid line) or below (triangles, dashed line) the canopy. See Table 2 for the parameter estimates associated with these variables.

Figure 6. (a) Effect of 1 min cicada playbacks on singing behaviour of seven common birds represented as the average (±SE) number of songs counted 1 min during or after the playback (PB), expressed as a difference from the number counted 1 min before the playback. (b) Songs counted during playbacks minus songs counted before playbacks, plotted against peak frequency of songs, with the frequencies covered by the cicada playback illustrated by a gradient bar. For species names see Appendix, Table A1.

Do Birds Partition Acoustic Space?

Similar to our findings, high levels of temporal and spectral overlap have previously been reported for avian participants in Neotropical dawn chorus (Luther, 2009; Planqué & Slabbekoorn, 2008). By contrast, at finer spatiotemporal scales and with smaller numbers of species, evidence of acoustic dispersion has been found amongst some members of avian assemblages (Ficken, Ficken, & Hailman, 1974; Knapton, 1987; Luther, 2009; Planqué & Slabbekoorn, 2008; Popp, Ficken, & Reinartz, 1985). Luther (2009) found that species in an Amazonian bird assemblage singing in the same 30 min interval and in the same forest stratum were more acoustically dispersed in comparison to those singing in different 30 min periods of the morning. Similarly, Planqué and Slabbekoorn (2008) found lower realized competition for acoustic space and reduced fine-scale temporal overlap between some species pairs in another Amazonian bird assemblage. They concluded that species whose call bandwidth falls within the most heavily used frequency range actively avoid overlap with each other. These results suggest that temporal partitioning of songs may only occur in communities or among conspecifics with high realized competition for acoustic space. In our study the temporal overlap between species suggests that interspecific competition for acoustic space
within this avian community may not be intense during the dawn chorus, perhaps because species avoid masking or interference by using unique spectrotemporal features in their songs. The low acoustic competition observed on BCI may also be a consequence of the overall low avian species diversity on this man-made island. Birds may also reduce acoustic overlap by utilizing low duty cycle songs (i.e. by giving repeated notes of short duration after periods of silence). However, given the number of species singing at the peak of the chorus, active temporal avoidance among all species would be difficult, if not impossible (e.g. Fig. 1).

Do Birds Avoid Nonavian Noise?

In general terms our results are consistent with the acoustic transmission hypothesis in that we found evidence of temporal avoidance of nonavian noise produced by insects. This hypothesis is usually invoked to account for the optimization of acoustic signals based on habitat structure; however, we found instead that nonavian biogenic noise (biophony) may play an important role in determining the timing of the dawn chorus. In the tropics, insects create a large amount of nonavian noise that falls within the frequency range used by some birds for acoustic communication. Our findings indicate that birds that use high-frequency calls or songs join the dawn chorus later than species calling at low frequencies. Those species singing at high frequencies do not begin singing until nocturnal insect noise has decreased in the morning.

Analysis of ambient noise at our site revealed a notable decrease (−20 dB) in background noise, corresponding mostly to a decrease in insect noise at 3.8 kHz and 6.1 kHz at dawn. This probably corresponded to a decrease in background noise from cricket or katydids species, which are known to have narrow-banded calls with dominant frequencies ranging from 3 to 9 kHz (Schmidt, Römer, & Riede, 2013). To avoid masking by nocturnal insects in their frequency range, birds may shift their call start times to periods of the morning when ambient noise at their peak frequency is lowest. Among the species recorded within the frequency range of the nocturnal insects, four species (spotted antbird, dot-winged antwren, black-cheeked woodpecker and red-capped manakin) began singing during time periods when ambient noise within their peak frequency range was at its minimum. Calling activity of crickets is mostly restricted to the night, peaks between 1800 hours and midnight, and declines subsequently, with katydids being the main source of nocturnally produced acoustic signals (Diwakar & Balakrishnan, 2007; Lang, Kalko, Römer, Bockholdt, & Dechmann, 2006; Lang et al., 2005). On BCI, Lang et al. (2006) found that background noise drops off at sunrise and quickly reaches a daytime level of 30–50 dB SPL below average night-time levels. By delaying their participation in the dawn chorus, birds with high-frequency songs avoid interference from nocturnal insects, effectively increasing the active space of their song. In addition, waiting for this frequency window to open may be particularly advantageous for birds singing at high frequencies, as higher-frequency songs suffer greater attenuation in tropical forest habitats (Marten, Quine, & Marler, 1977; Morton, 1975). In contrast to the decrease in high-frequency noise, ambient noise at lower frequencies (from 200 to 3000 Hz) tended to increase approximately 5 dB during our 1 h recordings (Fig. 4). Thus, those birds that join the dawn chorus early may also reduce interference from biotic noise caused by, for example, howler monkeys and other birds, such as parrots.

A variety of effects of abiotic noise on avian singing have been reported. For example, Ryan and Brenowitz (1985) found that birds in nonforest habitats in Gamboa, Panama avoided singing during times of the day when noise from wind was at its peak. More recently, effects of anthropogenic noise on bird acoustic communication have been noted. Along with detecting spectral changes in the acoustic properties (frequency, amplitude) of bird vocalizations in urban environments (Brumm, 2004; Slabbekoorn & den Boer-Visser, 2006), some studies have reported shifts in the timing of bird vocalizations in these environments (Fuller et al., 2007; Gil, Honarmand, Pascual, Pérez-Mena, & Macías García, 2015; Nordt & Klenke, 2013). For example, Fuller et al. (2007) found that European robins, Erithacus rubecula, initiate dawn chorus earlier in environments with louder anthropogenic ambient noise, after controlling for the effect of light pollution. Similarly, Gil et al. (2015) found that bird communities near airports shifted their songs earlier than those in neighbouring areas and these shifts were larger in species whose normal singing times overlapped with periods of aircraft noise. In contrast, examples of biotic noise influencing avian communication are rare. Slabbekoorn and Smith (2002) found differences in the minimum frequency of little greenbul song, Andropadus vires, across populations, which were associated with habitat-dependant shifts in biogenic noise levels in their frequency range. Additionally, Kirschel et al. (2009) reported that green hylia, Hylia prasina, sang at lower frequencies at sites with insect noise. As with anthropogenic noise, insect noise can alter the acoustic landscape and select for behaviours or acoustic properties that enable effective communication within avian communities.

Effect of Cicada Playbacks

To determine whether birds in the dawn chorus would actively alter their calling behaviour in response to temporary insect noise, we conducted cicada playbacks. Two different strategies were employed by species when presented with cicada playbacks. One species reduced its calling activity at sites with playbacks (collared forest-falcons; Supplementary Table S5). By contrast, three species singing in the same frequency range of cicadas reduced the rate at which they called during playbacks (cocoa woodcreeper, chestnut-backed antbird and white-flanked antwren; Fig. 6a) compared to calling before the playback. These qualitatively different responses probably have different causes. The decrease in call activity by collared forest-falcons at sites with playbacks suggests that these

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**Table 3**

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<th>Species</th>
<th>Peak frequency (Hz)</th>
<th>During–before</th>
<th>After–before</th>
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<tr>
<td>Rufous motmot</td>
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<td>1.22</td>
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<td>Collared forest-falcon</td>
<td>1214</td>
<td>−0.74</td>
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<td>2294</td>
<td>−2.19</td>
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<td>−3.18</td>
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<td>−3.73</td>
<td>0.45</td>
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</table>

Significant outcomes are shown in bold.

---
birds avoid noise by moving to other parts of their range where that noise is less common and communication can be more effective. Collared forest-falcons can range over 1000 ha (Thorstrom, 2007). In contrast, a reduction of calling activity only during playbacks by the three species with song frequencies that overlap cicada bouts could represent a strategy to mitigate losses associated with calling (such as energy, time lost from other activities or increased predation risk) when faced with broadband noise that could temporarily reduce communication effectiveness drastically. Such flexible calling behaviour could be an important strategy for species with small home ranges. Nevertheless, these short-term behavioural responses to cicada playbacks indicate that some birds actively avoid call masking by nonavian noise.

Similar short-term responses to noise have been observed in other species. Strawberry poison-dart frogs, *Oophaga pumilio*, show a similar inhibitory response to cicada choruses and respond less to playbacks of conspecifics when cicadas are calling in the background (Paez, Bock, & Rand, 1995). To avoid masking by acoustically dominant heterospecifics, birds in temperate forests have been found to insert their songs directly after songs of dominant species (Ficken et al., 1974; Popp et al., 1985). To mitigate the influence of temporary ambient noise, two additional mechanisms have been observed in avian species: the addition of extra syllables in a call series (e.g. Lengagne, Aubin, Lauga, & Jouventin, 1989; Potash, 1972) or amplitude modulation of vocalizations, termed the Lombard effect (e.g. Brumm, 2004; Brumm & Todt, 2002). To our knowledge, neither of these short-term mechanisms to avoid interference has been examined with respect to insect noise before.

Although these results suggest that nonavian biological noise can have important effects on avian acoustic communication, extrapolating from these playback results should be done with caution. We only counted species that sang frequently and whose songs could be detected in spectrograms during cicada calling bouts. Species that called less often would be difficult to hear or identify in spectrograms during playback periods. Therefore, we cannot conclude that all species with high-frequency songs actively avoid cicada noise. In addition, our methods only monitored the behaviour of senders and the effect of noise on signal active space. The responsiveness of receivers could also be an important factor influencing sender calling behaviour in a noisy environment and warrants further investigation.

**Conclusions**

The acoustic transmission hypothesis has most often been used to explain why dawn is a favourable climatic period of the day to produce vocalizations. This hypothesis has not previously been invoked to explain interspecific variation in when individuals should join a dawn chorus. By considering the possibility that biotic noise varies by frequency over time, especially at dawn, we discovered that the time when a bird species joins the dawn chorus can be predicted by the frequency of its song and associated temporal noise profile. We did not find evidence of acoustic avoidance of avian noise, as we had initially predicted, possibly because the songs of most species have sufficiently unique spectrotemporal features to make them distinguishable within the chorus of this community. Instead, we found evidence of nonavian noise avoidance during dawn chorus. In particular, birds with high-frequency songs began singing later once the noise profile of those frequency ranges had decreased due to a reduction in acoustic signals produced by insects. Birds with low-frequency songs joined the chorus earlier before ambient noise at their frequencies increased at dawn. Active avoidance of insect noise was demonstrated by our playback experiment in which birds that call in the frequency range of emerald cicadas significantly reduced their calling activity during playbacks of cicada calls. These results highlight the potential importance of the entire tropical forest acoustic community in shaping the avian dawn chorus. Given that this study only assessed the influence of nonavian noise on the dawn chorus at one location and period, considering additional sites and seasons with different noise profiles would provide further insight into the influence of nonavian noise on the acoustic properties of avian assemblages.

**Acknowledgments**

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**Supplementary Material**

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2015.12.003.

**References**


APPENDIX

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<tr>
<th>Common name</th>
<th>Code</th>
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<tr>
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