



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, *Zammaria 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

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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 & Yezerinac, 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; Krams, 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 decodability (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/brp/raven/ravenversions>) using a Hann window, FFT = 4096 and

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