

Contrasting acoustic-space competition avoidance strategies in Afrotropical forest birds



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ARTICLE INFO

Article history:

Received 26 February 2023

Initial acceptance 1 May 2023

Final acceptance 1 December 2023

MS. number: 23-00099R

Keywords:

acoustic interference

acoustic partitioning

Kibale National Park

signal space

Uganda

Acoustic signals are of critical importance to songbirds which rely on them for mate attraction and territorial defence. Interference caused by sounds that overlap in frequency and time can disturb or mask signal detection. While species differ in their song spectral properties, duration and composition, the limited acoustic space may lead to evolution of behavioural strategies aimed at minimizing competition. Using playback experiments we tested whether tropical forest songbirds use temporal or spectral avoidance to reduce competition for acoustic space. We focused on two species with different song spectral ranges: green-backed camaroptera, *Camaroptera brachyura*, with a broad-spectrum song, and scaly-breasted illadopsis, *Illadopsis albipectus*, which produces a narrow-spectrum song. We found that scaly-breasted illadopsis avoided both temporal and spectral overlap. By contrast, in green-backed camaroptera, there was no difference in the number of songs produced between the periods of silence and noise. However, when we varied the frequency of the noise, green-backed camaroptera increased the song rate during the playbacks of noise with maximal spectral overlap, suggesting increasing signal redundancy. Our results show that competition avoidance strategies may be species specific and could be related to the spectral frequency range of the species.

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Many animals use acoustic advertisement signals to attract mates and repel rivals (Bradbury & Vehrencamp, 2011). The acoustic space is a common resource shared by all animals in a community and can be partitioned along two primary axes: spectral and temporal (Nelson & Marler, 1990; Planqué & Slabbekoorn, 2008). When vocalizations of two individuals overlap in time and frequency, the resulting acoustic interference can mask or alter the signal (Dooling, 1982; Klump, 1996). In the case of advertisement signals, this can lead to reduced reproductive success (Bradbury & Vehrencamp, 2011). Thus, according to the acoustic partitioning hypothesis (Hödl, 1977) animals should employ acoustic-space competition avoidance strategies that minimize signal interference.

To reduce competition for acoustic space between coexisting species, animals such as amphibians, fishes, insects, birds and mammals can vocalize in different locations (i.e. spatial separation; Nemeth et al., 2002; Jain & Balakrishnan, 2012; Lima et al., 2019), alter the timing of their signals (temporal avoidance) by vocalizing in different seasons or at different times of day (Luther, 2008;

Wilson et al., 2020), or in the intervals between the vocalizations of other species (Bleach et al., 2015; Brumm, 2006; Cody & Brown, 1969; Herrick et al., 2018). Over time, species can also evolve divergent spectral frequencies to those of other species in their acoustic community (spectral separation), so that different species can simultaneously occupy different bands along the frequency spectrum (i.e. spectral avoidance; Kirschel et al., 2009; Krishnan & Tamma, 2016; Villanueva-Rivera, 2014). By contrast, some species show vocal plasticity that can enable individuals to actively modify their signal frequency by shifting their signals above or below the frequency band of the interfering sound (i.e. spectral adaptation; Lopez et al., 1988).

Birds are one of the most vocal taxonomic groups, producing songs to attract mates and defend territories (Pearse et al., 2018). Those inhabiting tropical forests are challenged with a particularly complex acoustic environment (Brumm & Slabbekoorn, 2005), with diverse vocalizing animals including amphibians, insects and mammals (Gerhardt & Huber, 2003; Rogers & Kaplan, 2000). Thus, birds must compete for acoustic space not only with other bird species (Bolanos-Sittler et al., 2021; Hart et al., 2021; Luther, 2009), but also with other taxa (Hart et al., 2015; Stanley et al., 2016). Additionally, year-round territoriality, an extended breeding season

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or asynchronous breeding can lead to many tropical forest birds singing year-round (Lefebvre et al., 1992; Rowan, 1966). This may affect the intensity of interspecific competition for acoustic space, as unlike in the northern temperate regions, the species are not restricted to singing in a short seasonal window with the onset of spring.

In tropical bird communities specifically, studies have suggested different niche-partitioning strategies employed by species to reduce interspecific acoustic-signal interference. These include temporal avoidance (Hart et al., 2021), spectral avoidance (Kirschel et al., 2009), spatial separation (Chitnis et al., 2020) or a combination of these strategies (Luther, 2009). Yet, there is mixed support for an acoustic niche-partitioning hypothesis in tropical birds. For example, Planqué and Slabbekoorn (2008) found little evidence of competition avoidance, except at the frequencies most commonly used by most birds, Tobias et al. (2014) showed that, rather than separating acoustically, bird species with similar songs use the interspecific social information and aggregate in time and space, while Alquezar et al. (2020) found no consistent temporal shifts in the timing of the tropical bird dawn chorus to avoid airport noise. Nevertheless, studies have primarily relied on descriptive investigations of spectral segregation and temporal avoidance in birds, proposing hypotheses for acoustic space partitioning which should be examined experimentally.

Here we tested two hypotheses for the behavioural mechanisms used to avoid competition for acoustic space in two species of small tropical-forest passerines with different song structure and frequency range. If the birds use temporal avoidance, we predicted that they would produce fewer songs when experimental white noise broadcast into their territory matched their song frequency range than in the periods of no experimental noise. To test for spectral avoidance, we broadcast continuous noise in frequencies alternately above, matching or below the frequency range of the species song, predicting that the birds would produce fewer songs in the periods of noise matching their natural frequency range.

METHODS

Study Site and Species

Kibale National Park (766 km²) is in western Uganda (0°13'N–0°41'N and 30°19'E–30°32'E), near the foothills of the Ruwenzori Mountains. The park contains a moist evergreen rainforest at elevations ranging between 1110 and 1590 m (Latja et al., 2016). The mean daily minimum and maximum temperatures are 15.5 °C and 23.7 °C, respectively, with mean annual rainfall of 1664 mm (data from 1974–1996, Chapman et al., 2000), and a dry season between June and August. The forest supports around 375 species of birds and 350 species of trees (Dranzoa, 2001). Our study site was located near Kanyawara in the northwestern section of the park, with a mosaic of mature primary forest, secondary forest, swamp forest and grassland (Sekercioglu, 2002).

We conducted our study in the dry season (June 2022) on two passerine species found in Kibale National Park: the green-backed camaroptera, *Camaroptera brachyura* (Cisticolidae) and the scaly-breasted illadopsis, *Illadopsis albipectus* (Pellorneidae; Fig. 1a, b). Both species are sedentary and occupy small territories in the undergrowth and lower levels of the forest (Stevenson & Fanshawe, 2020).

Scaly-breasted illadopsis are restricted to rainforests at 700–2100 m altitude in the central part of tropical Africa, with a distribution range extending from western Kenya to northwestern Angola (Collar & Robson, 2020). Males sing and maintain their

territories all year round, and the species appears to breed throughout the year (Lindsell et al., 2007). Scaly-breasted illadopsis sing most actively in the 2 h after dawn from the core of their territory, then they forage for the rest of the day (Lindsell, 2001b). Their song has a narrow frequency spectrum range (2.48–2.77 kHz) and consists of two or three loud, slowly delivered, rising notes (Fig. 1c), produced at a rate of 8–10 songs/min (Lindsell, 2001a).

Green-backed camaroptera are habitat generalists commonly found throughout sub-Saharan Africa in forest undergrowth, as well as in dense bushes, gardens and cultivated areas at altitudes of up to 2200 m (Ryan, 2020). The song of this species has a broad frequency spectrum range (1.22–5.95 kHz) and consists of loud cracking notes produced in series lasting 1–3 s, often repeated over several minutes (Fig. 1d; Ryan, 2020).

Stimuli

We collected reference recordings of bird songs in Kibale National Park between 18 and 30 November 2021. We recorded six naturally singing green-backed camaroptera and five scaly-breasted illadopsis between 0700 and 1030, using a Rode NTG8 shotgun microphone (frequency response 40 Hz–20 kHz; 20.0 dB, 1 V/Pa (97.5 mV at 94 dB SPL) ± 2 dB at 1 kHz) connected to a Sound Devices MixPre 3 recorder. Using Raven Pro v1.6.1 software (<https://ravensoundsoftware.com/>) we measured between 5% and 95% of the total energy distributed in the songs (12 ± 6 songs per individual, range 3–20 songs, see Supplementary material for more details). We found that 90% of the energy of the signal of green-backed camaroptera is distributed between 1.99 ± 0.32 and 4.92 ± 0.58 (mean ± SD) kHz, while in scaly-breasted illadopsis it is between 2.55 ± 0.03 and 2.73 ± 0.03 kHz. We used this information to prepare the playback files for the two experiments using Avisoft SasLab Pro v5.2.12 (<https://www.avisoft.com/>).

To test for temporal avoidance, we prepared playback files (wav, sampling rate 22 kHz with 16-bit accuracy), with two experimental treatments: 5 min of white noise in the frequency range covering 5–95% of the tested species' frequency (1.75–5.35 kHz for green-backed camaroptera, 2.25–2.85 kHz for scaly-breasted illadopsis), and 5 min of silence (Fig. 2a). Each experiment lasted 60 min, with each treatment repeated six times and presented to the tested bird randomly in an order starting with either noise–silence or silence–noise.

To test for spectral avoidance, we prepared playback files (wav, sampling rate 22 kHz with 16-bit accuracy) of continuous noise with three treatments of equal frequency bandwidth (Fig. 2b): 5 min of white noise in the frequency range below the lower 5% frequency of the tested species ('lower', 0–1.75 kHz for green-backed camaroptera, 1.65–2.25 kHz for scaly-breasted illadopsis); 5 min of white noise in the frequency range overlapping 5–95% frequency of the tested species ('matching', 1.75–5.35 kHz for green-backed camaroptera, 2.25–2.85 kHz for scaly-breasted illadopsis); and 5 min of white noise in the frequency range above the upper 5% frequency of the tested species ('higher', 5.35–8.95 kHz for green-backed camaroptera, 2.85–3.45 kHz for scaly-breasted illadopsis). Each experiment lasted 75 min, with each treatment repeated five times and presented to the tested bird randomly in one of six predefined orders (Table A1).

Procedure

We carried out the experiments in the dry season, between 1 and 28 June 2022, between 0655 and 0935 (scaly-breasted illadopsis) and between 0722 and 1130 (green-backed camaroptera),

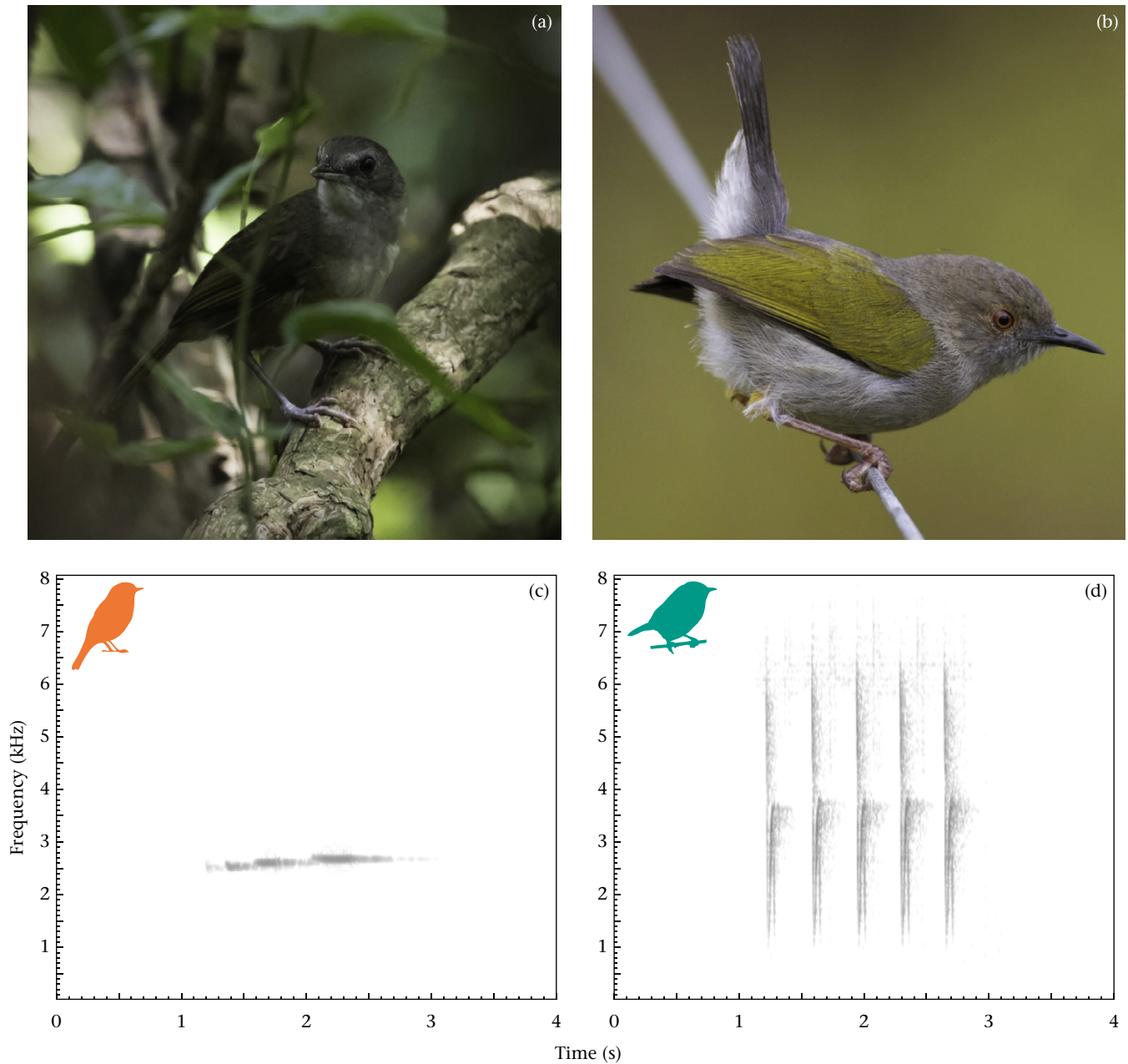


Figure 1. The two study species: (a) scaly-breasted illadopsis, *Illadopsis albipectus* (photo: Chris Sloan) and (b) green-backed camaroptera, *Camaroptera brachyura* (photo: Chris Sayers). Spectrograms with examples of the songs of (c) scaly-breasted illadopsis and (d) green-backed camaroptera. Sampling rate 48 kHz; FFT size 1024; Hanning window; overlap 75%.

which corresponded to the observed time of peak vocal activity for each species during the study period. Both experiments concurrently tested one to two different birds per morning, and to reduce habituation we ensured that neighbouring birds were not tested on consecutive days, and that birds tested on the same day were out of earshot from each other. The experimental set-up was similar in both experiments, differing only in the number of speakers used. Owing to the limited number of speakers available, we used six of them when testing for spectral avoidance, and five when testing for temporal avoidance.

We searched for singing birds from forest trails and when found we observed the bird for 10–15 min to locate its core singing territory. We positioned one ‘central’ speaker (JBL Charge 5) on a tree

branch approximately 4 m above ground at the centre of the territory and placed a further four or five ‘edge’ speakers 20 m away from the centre in different directions surrounding the core territory, all connected to the central speaker via Bluetooth (Fig. 2c). After setting up the speakers and ensuring that the tested bird was still singing within the speaker range, we waited 5 min before starting the experiment. The playback sound was played simultaneously from all connected speakers, each set at 90 ± 2 dB at 1 m. Two observers recorded the experiment. One observer stayed stationary near the centre of the territory using a Rode NTG8 shotgun microphone (frequency response 40 Hz–20 kHz; 20.0 dB, 1 V/Pa (97.5 mV at 94 dB SPL) ± 2 dB at 1 kHz) connected to a Sound Devices MixPre 3 recorder. The other observer moved within and

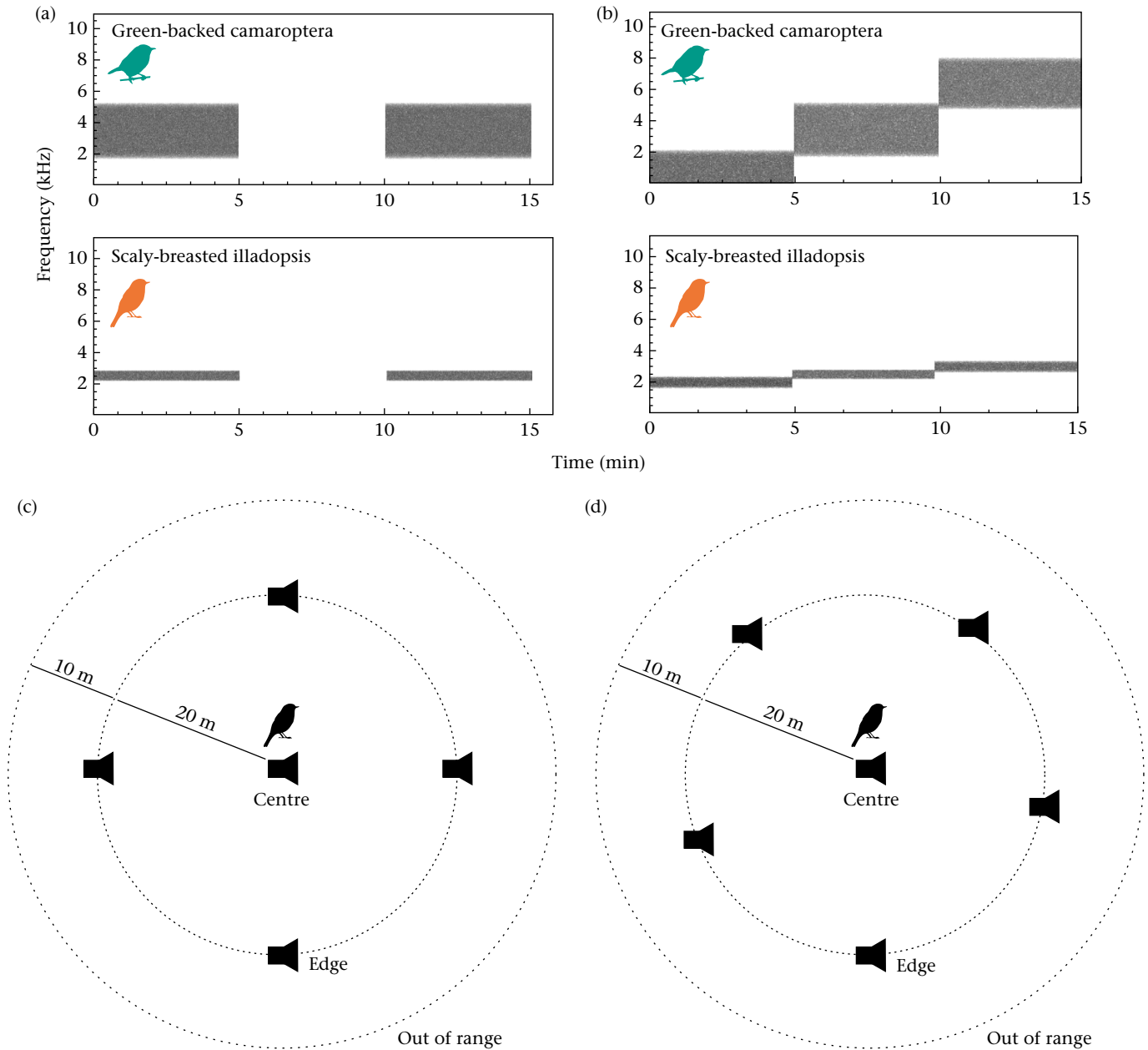


Figure 2. Example spectrograms of the 15 min sections of the white noise playback files used to test for (a) temporal avoidance (noise–silence–noise) and (b) spectral avoidance (lower–matching–higher) in green-backed camaroptera, *Camaroptera brachyura*, and scaly-breasted illadopsis, *Illadopsis albipectus*, and the experimental set-ups for testing (c) temporal avoidance and (d) spectral avoidance.

outside the speaker range as necessary to determine the location of the tested bird, while recording with an Olympus LS-12 handheld recorder with built-in stereo microphones. Each observer counted and recorded every song produced by the tested bird that they could hear, as well as whether the bird was within the range marked by the speakers, defined as up to 10 m away from an edge speaker (Fig. 2d). To record any songs that may be inaudible to the observers, we placed one Song Meter Mini (Wildlife Acoustics) recorder with a single built-in omnidirectional microphone (signal to noise ratio 78 dB at 1 kHz; sensitivity $+6 \text{ dB} \pm 4 \text{ dB}$ at the 18 dB gain setting used) within the territory, but away from the stationary observer. Each experiment was carried out entirely by the same stationary observer (A.S. or E.S.) and the same moving observer (P.R. or S.K.).

In the experiment testing for temporal avoidance, we tested 20 green-backed camaroptera individuals and 20 scaly-breasted illadopsis individuals, with equal number of birds of each species presented with each playback order. In the experiment testing for spectral avoidance, we tested 22 green-backed camaroptera individuals and 18 scaly-breasted illadopsis individuals. To minimize any effects of the playback on individual birds, we tested 41 green-backed camaroptera in total, with only one individual tested in both experiments. Owing to a smaller number of scaly-breasted illadopsis available, we tested 30 birds of this species in total, with eight individuals tested in both experiments. When the same bird was tested twice, we ensured the two experiments were performed more than 3 days apart. All experiments performed in 1 day were done out of earshot of other birds tested on the same day.

Acoustic Analysis

All experiments were recorded in wav format at sampling rate 48 kHz with 16-bit accuracy. We manually aligned the recordings from each tested bird and saved it as a single synchronized three-channel wav file using Audacity v3.1.3 software (<https://audacityteam.org>). We then manually scanned each three-channel recording using Raven Pro software and counted the songs the bird produced during each of the 5 min treatments, noting the position of the bird (within range or out of range of the speakers) during each treatment. We scanned all three channels to ensure that we included all the songs produced by the tested bird as it was moving throughout its territory.

Statistical Analysis

All analyses were performed in R v4.2.1 (<https://www.R-project.org>). To demonstrate the association between the bird's location and the duration of the experiments we used logistic regression models (glm function; binomial family, logit link). We set the response variable as binary (inside or outside the speaker range) during each 5 min treatment, while the predictor variables were: (1) the sequential number of the 5 min treatments throughout the experiment; and (2) the treatment type (either noise or silence in the temporal avoidance experiment or lower, matching or higher frequency noise in the spectral avoidance experiment).

To test the effect of either silence or noise on the number of songs produced by the birds (temporal avoidance) we used generalized linear mixed models (GLMMs; negative binomial distribution, log link) for each species using the glmmTMB package (Brooks et al., 2017). Odds ratios were calculated with the emmeans v1.8.7 package (Length, 2023). We set the number of songs produced by the bird during the 5 min treatment as the response variable, and the treatment (noise or silence) and sequence of the 5 min playbacks as predictor variables (fixed effects). Since a large proportion of scaly-breasted illadopsis moved outside the range throughout the playback experiment, we additionally set the location (inside or outside range) as a fixed effect. The identity of the bird was set as a random effect in the models.

We prepared similar GLMMs to test the effect of the noise frequency range on the number of songs produced by the birds (spectral avoidance). We set the number of songs produced by the bird during the 5 min treatment as the response variable, and the treatment (lower, matching or higher noise) and sequence of the 5 min playbacks and location (inside or outside range) as predictor variables (fixed effects). The identity of the bird was set as a random effect in the models.

We tested whether the overall effect of the experiment, noise and silence in the temporal avoidance experiment and continuous noise of either lower, matching or higher frequency in the spectral avoidance experiment, affected the species' song rate during the noise of matching frequency. Here we used GLMMs setting the number of songs produced by the bird during the 5 min matching noise treatment as the response variable and the experiment (noise–silence or continuous noise) and sequence of 5 min playbacks as predictor variables (fixed effects). The identity of the bird was set as a random effect in the model.

Ethical Note

All research procedures were approved by the Uganda Wildlife Authority (COD/96/05) and the Uganda National Council for Science and Technology (NS302ES). All procedures were noninvasive and did not require an additional ethical approval, in accordance with the research guidelines of AMU and ASAB/ABS.

RESULTS

Temporal Avoidance

Green-backed camaroptera individuals stayed within the speaker range during nearly all treatment sessions, with only one individual leaving the range for 5 min at the start of the experiment (Fig. A1). There was no significant difference in the number of songs produced during the periods of silence (mean \pm SD = 13.0 \pm 17.1 songs; Fig. 3a) and white noise matching the species' song frequency range (mean \pm SD = 14.2 \pm 19.3 songs; P = 0.684; Table 1, Fig. 4). There was also no significant effect of the experiment duration on the number of songs (P = 0.658).

Scaly-breasted illadopsis individuals always sang from the core of the territory at the start of the experiment but moved around and outside the range throughout the experiment. There was a significant effect of the duration of the experiment on bird location, with fewer birds remaining within the speaker range during subsequent 5 min treatment intervals (odds ratio, OR = -0.28; 95% confidence interval, CI = -0.8, -0.9; P < 0.001; Fig. A1), but no significant effect of the presence or absence of noise on the bird's location (P = 0.882). The birds sang significantly more during the silent periods (mean \pm SD = 20.6 \pm 18.9 songs; OR = 1.86; 95% CI = 1.25, 2.76; P < 0.01; Fig. 4, Table 1) than during the periods of white noise matching their song frequency (mean \pm SD = 14.3 \pm 17.6 songs; Fig. 3c). There was also a significant effect of experiment duration, with the birds producing significantly fewer songs during the later 5 min treatment intervals (OR = 0.85; 95% CI = 0.79, 0.91; P < 0.001), but no significant effect of the bird's location on the number of songs produced (P = 0.414; Fig. 4).

Spectral Avoidance

Green-backed camaroptera individuals stayed primarily within the range of the speakers and there were no significant effects of the duration of the experiment (P = 0.773) or the noise frequency (P = 0.999) on the bird's location relative to the speaker range (Fig. A1). The birds produced significantly fewer songs during the periods of noise above their song frequency range (mean \pm SD = 11.5 \pm 14.3 songs; OR = 0.47; 95% CI = 0.26, 0.76; P < 0.01; Table 2, Fig. 5) than during the periods of white noise matching their song frequency (mean \pm SD = 23.4 \pm 22.9 songs; Fig. 3b). There was no significant difference between the number of songs produced during the noise matching the species frequency range and the periods of noise below their song frequency range (mean \pm SD = 19.2 \pm 21.6 songs; P = 0.481), and no significant effect of the experiment duration (P = 0.209) or the bird's location (P = 0.083) on the number of songs produced (Table 2, Fig. 5).

Scaly-breasted illadopsis individuals always sang from the core of the territory at the start of the experiment, but often moved around and sometimes out of range through the experiment. There was a significant effect of the duration of the experiment on the bird's location, with fewer birds remaining within the speaker range during subsequent 5 min treatment intervals (OR = -0.15; 95% CI = -0.22, -0.07; P < 0.001; Fig. A1), but no significant effect of noise frequency on the bird's location (P = 0.999). The birds produced significantly more songs during the periods of noise above (mean \pm SD = 16.9 \pm 17.4 songs; OR = 1.71; 95% CI = 1.08, 2.70; P < 0.05) and below (mean \pm SD = 15.8 \pm 15.7 songs; OR = 1.64; 95% CI = 1.02, 2.62; P < 0.05; Fig. 5, Table 2) their frequency range than during the periods of white noise matching their song frequency (mean \pm SD = 12.6 \pm 16.5 songs; Fig. 3d). There was also a significant effect of experiment duration, with the birds producing significantly fewer songs during the later 5 min treatment intervals (OR = 0.84; 95% CI = 0.79, 0.88; P < 0.001), but no

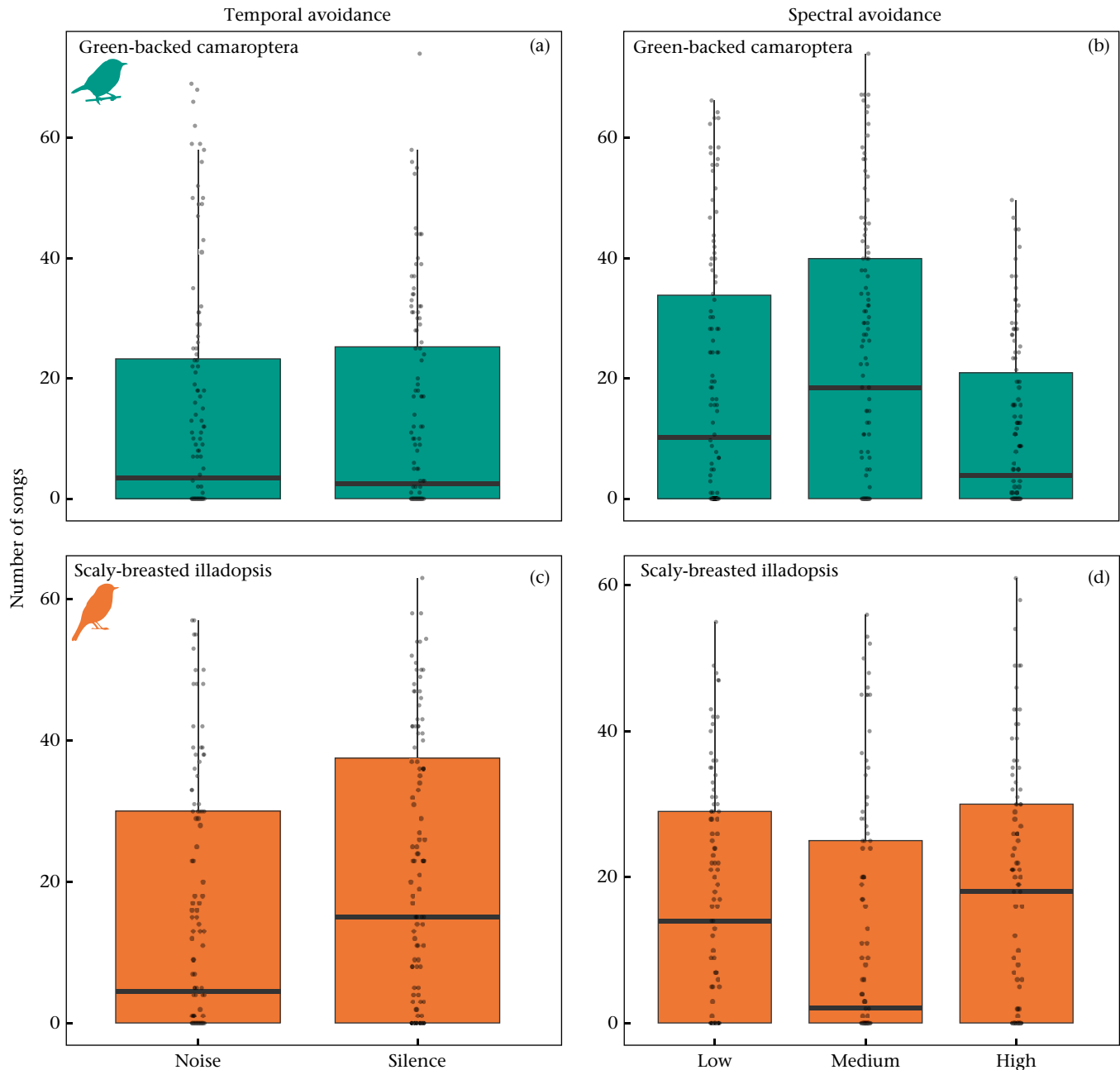


Figure 3. Results of the experiments testing temporal and spectral avoidance hypotheses. Number of songs produced by (a) 20 green-backed camaroptera, *Camaroptera brachyura*, and (c) 20 scaly-breasted illadopsis, *Illadopsis albipectus*, during the 5 min periods of white noise matching their song frequency range and 5 min periods of silence. Number of songs produced by (b) 22 green-backed camaroptera and (d) 18 scaly-breasted illadopsis during the 5 min periods of white noise below their song frequency range (low), matching their song frequency range (medium) and above their song frequency range (high). The boxes depict the 25th percentiles, median line and 75th percentiles and the whiskers represent 95% confidence intervals. The dots represent individual data points tallying the number of songs per 5 min interval.

significant effect of the bird's location ($P = 0.138$; Fig. 5) on the number of songs produced.

Song Rate Comparison Between Experiments

Although green-backed camaroptera individuals generally produced more songs during the noise matching its song frequency range in the experiment examining spectral avoidance in continuous noise (mean \pm SD = 23.4 ± 22.9 songs) than during the noise matching its frequency in the temporal avoidance experiment presenting noise and silence (mean \pm SD = 14.2 ± 19.3 songs), this

difference was not significant ($P = 0.070$; Fig. 3, Table A2). There was no significant difference between the two experiments in the number of songs produced by scaly-breasted illadopsis individuals during the matching frequency noise ($P = 0.85$; Table A2).

DISCUSSION

The two species we tested showed different song rate production responses to the introduction of competing acoustic signals. Scaly-breasted illadopsis sang significantly less in the noise masking their song than when no noise was broadcast. When noise was

Table 1
Results of the temporal avoidance experiments

| | Coefficients | Estimate | SE | Z | P |
|---------------------------|---------------------|----------|-------|--------|--------|
| Green-backed camaroptera | Intercept | 2.492 | 0.355 | 7.021 | <0.001 |
| | Treatment (silence) | −0.117 | 0.287 | −0.407 | 0.684 |
| | Sequence | 0.019 | 0.043 | 0.443 | 0.658 |
| Scaly-breasted illadopsis | Intercept | 3.299 | 0.295 | 11.183 | <0.001 |
| | Treatment (silence) | 0.620 | 0.201 | 3.084 | 0.002 |
| | Sequence | −0.162 | 0.035 | −4.554 | <0.001 |
| | Location (outside) | −0.245 | 0.300 | −0.817 | 0.414 |

GLMMs examining the effects of: (1) experimental treatment and sequence of the 5 min treatment interval in green-backed camaroptera, *Camaroptera brachyura*, and (2) the experimental treatment, the sequence of the 5 min treatment interval and the bird's location relative to the playback range in scaly-breasted illadopsis, *Illadopsis albipictus*, on the number of songs produced.

presented throughout the experiment, the species tended to produce more songs in the periods when the noise did not overlap with its song frequency range. Our results thus support the hypothesis that scaly-breasted illadopsis use temporal and spectral avoidance to reduce the competition for acoustic space. This provides experimental evidence to support previous, predominantly descriptive studies, demonstrating that birds can adjust the timing of their songs to avoid spectral overlap with other sounds (Brumm, 2006; Brumm & Slabbekoorn, 2005; Cody & Brown, 1969; Ficken et al., 1974; Hart et al., 2015; Planqué & Slabbekoorn, 2008).

Conversely, we found no evidence of temporal and spectral avoidance in response to competing noise in green-backed camaroptera. Green-backed camaroptera sang more during the matching frequency noise presented in the experiment with continuous noise than during the matching frequency noise that was interspersed with periods of silence, although the difference in song number between the experiments was marginally nonsignificant. While there was also no significant difference between the number of songs the species produced in the continuous noise of lower and matching spectral frequency, the birds sang significantly less when the broadcast noise was above their song frequency range than when it was overlapping. Increased song production while an overlapping frequency is audible is consistent with the signal redundancy hypothesis (Brumm & Slater, 2006; Lengagne et al., 1999; Wiley & Richards, 1982). Given this scenario, under acoustic conditions that limit signal transmission in a given frequency range, individuals increase the rate of signal production, thus increasing the chance that the signal reaches the receiver. This could also potentially result in the apparent increased singing response in noisy conditions observed in green-backed camaroptera during both the matching and lower frequency noise, as seen in serins, *Serinus serinus*, which increase vocalization rate in response to anthropogenic noise (Díaz et al., 2011).

Alternative strategies for competition avoidance not tested in our study could also potentially explain the differences in behaviours between the two species. Owing to the interference of our experimental noise we could not measure the spectral frequencies of songs produced in response to the playbacks, and therefore did not test for spectral adaptation, i.e. modifying the song frequency to avoid competing noise, as a possible behavioural strategy for competition avoidance (Goodwin & Podos, 2013; Lopez et al., 1988). Both green-backed camaroptera and scaly-breasted illadopsis have simple, stereotyped songs, with little spectral variety observed within or between individuals. We also set the frequency of our experimental matching noise to overlap all of our recorded reference songs to ensure maximum spectral overlap. While we did not observe obvious song frequency shifts and changes in the degree of overlap with matching noise during the playbacks in either species, it is possible that green-backed camaroptera could adjust their spectral frequency rather than reduce song rate during periods of overlapping noise. Furthermore, rather than reducing the singing

output in response to noise, birds can also increase the amplitude of their vocalizations to mitigate the masking effect of the competing sound (Brumm, 2004; Kunc & Schmidt, 2021; Nemeth et al., 2013). We did not measure the song amplitude of the tested birds, but such a response could possibly explain the lack of singing rate change observed in green-backed camaroptera. Further studies focusing on spectral adaptation and song amplitude changes are needed to determine whether green-backed camaroptera can also modify their song frequency or amplitude in response to acoustic interference.

One of the behavioural responses to a competing sound can be changing location by moving away from the source of the interfering noise. For example, studies have found similarly singing birds broadcasting from different perch heights (Chitnis et al., 2020), and acoustically similar frog species inhabiting different pools (Lima et al., 2019). While green-backed camaroptera usually stayed within the playback range throughout the experiment, scaly-breasted illadopsis tended to move away throughout the experiment, but we found this behaviour to be affected by the increasing duration of the experiment, rather than the playback noise treatment. This is consistent with Lindsell (2001b), who noted that scaly-breasted illadopsis produce most songs in the core of their range in the first 30 min after dawn, after which the singing intensity starts to decrease, and the birds begin foraging further from the core within 2 h. Thus, while moving out of range in response to the noisy playback is possible, leaving its core range may also be a routine behaviour of the species. The decrease in song rate in subsequent playback treatments may also be due to difficulties in detecting the species' songs at a greater distance, particularly during the noisy playback. Using the three-channel recordings from different locations within the range, we aimed to capture all songs produced during the experiment, but it is possible that some songs produced away from all the recording devices were missed.

The songs of the two species differ in both spectral range and song structure. Scaly-breasted illadopsis produce short songs in the narrow frequency range which can overlap and be masked by many other forest species (Mikula et al., 2021; Planqué & Slabbekoorn, 2008), while there are fewer animals producing broad-spectrum sounds which could fully overlap with the longer, broad-spectrum songs of green-backed camaroptera (Hart et al., 2021; Weir et al., 2012). Thus, even if another singing species temporally overlaps with the green-backed camaroptera, it is unlikely to fully cover its song frequency spectrum, resulting in different behavioural reactions to song masking observed in the two species.

An example of an animal that produces continuous, loud, broad-spectrum vocalizations that can overlap and mask bird songs are the cicadas (Hemiptera, Cicadidae). In response to cicadas, neotropical birds start singing earlier at dawn (Stanley et al., 2016) and often stop singing at the onset of cicada vocalizations later in the morning, with only birds with songs not overlapping those of cicadas continuing to sing (Hart et al., 2015). The higher-frequency

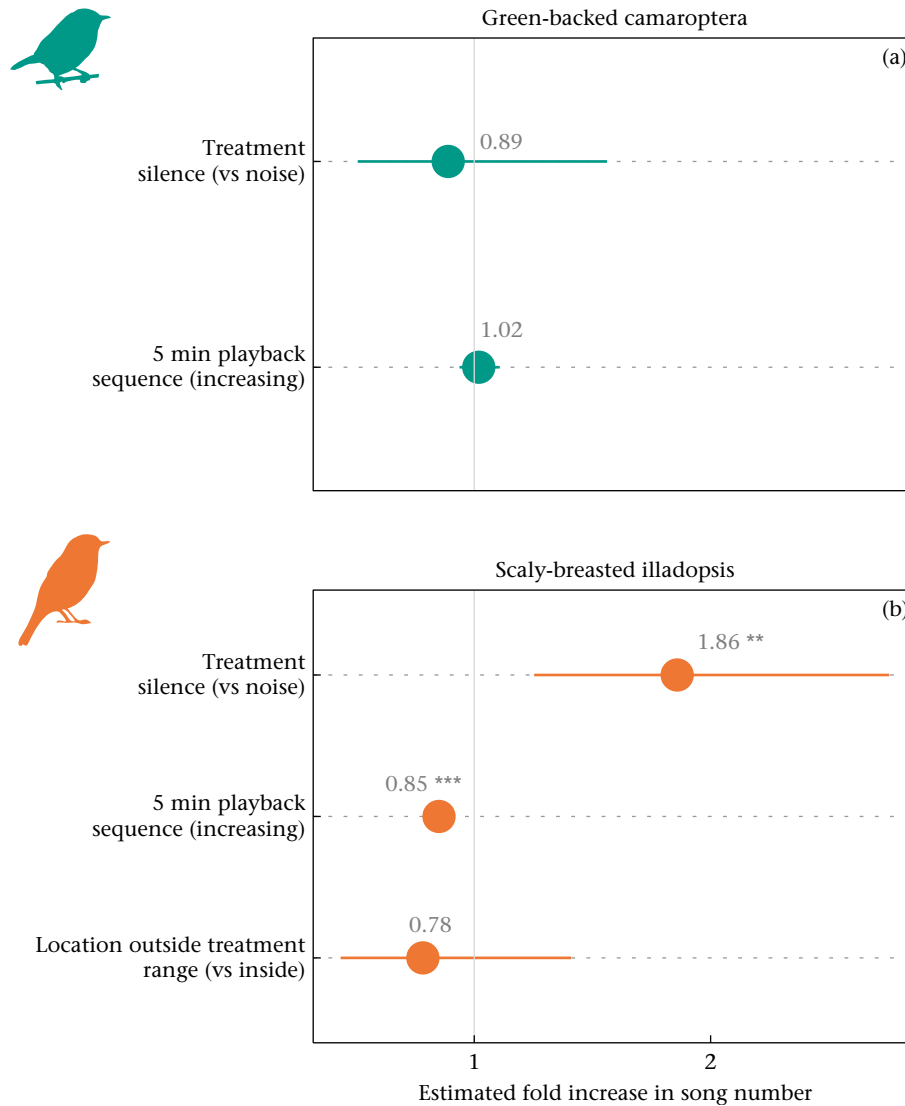


Figure 4. Odds ratios (ORs) of fixed effects estimates from the GLMMs predicting the difference in song rate in periods of silence compared to experimental white noise matching the species' song frequency in (a) 20 green-backed camaroptera, *Camaroptera brachyura*, and (b) 20 scaly-breasted illadopsis, *Illadopsis albipectus*, with increasing experiment duration in both species, and when the bird was outside the speaker range compared to within the range of the speakers in scaly-breasted illadopsis. ** $P < 0.01$; *** $P < 0.001$. Bars represent 95% confidence intervals. Full model output is given in [Table 1](#).

Table 2
Results of the spectral avoidance experiments

| | Coefficients | Estimate | SE | Z | P |
|---------------------------|--------------------|----------|-------|--------|--------|
| Green-backed camaroptera | Intercept | 3.249 | 0.283 | 11.500 | <0.001 |
| | Treatment (higher) | -0.760 | 0.250 | -3.033 | 0.002 |
| | Treatment (lower) | -0.175 | 0.248 | -0.705 | 0.481 |
| | Sequence | -0.030 | 0.024 | -1.256 | 0.209 |
| | Location (outside) | 0.694 | 0.340 | 1.735 | 0.083 |
| Scaly-breasted illadopsis | Intercept | 3.106 | 0.387 | 8.021 | <0.001 |
| | Treatment (higher) | 0.536 | 0.233 | 2.295 | 0.022 |
| | Treatment (lower) | 0.493 | 0.240 | 2.058 | 0.040 |
| | Sequence | -0.180 | 0.026 | -6.89 | <0.001 |
| | Location (outside) | 0.524 | 0.353 | 1.485 | 0.138 |

GLMMs examining the effects of experimental treatment, sequence of the 5 min treatment interval and the bird's location relative to playback range on the number of songs produced by 22 green-backed camaroptera, *Camaroptera brachyura*, and 18 scaly-breasted illadopsis, *Illadopsis albipectus*.

broad-spectrum white noise we presented to the green-backed camaroptera (5.35–8.95 kHz) matched that of some of the cicada species vocalizing at the study site during the experiments

(approximately 5.5–8.0 kHz). Furthermore, unlike in the case of scaly-breasted illadopsis, the singing activity of green-backed camaroptera is not restricted to early mornings and the species is

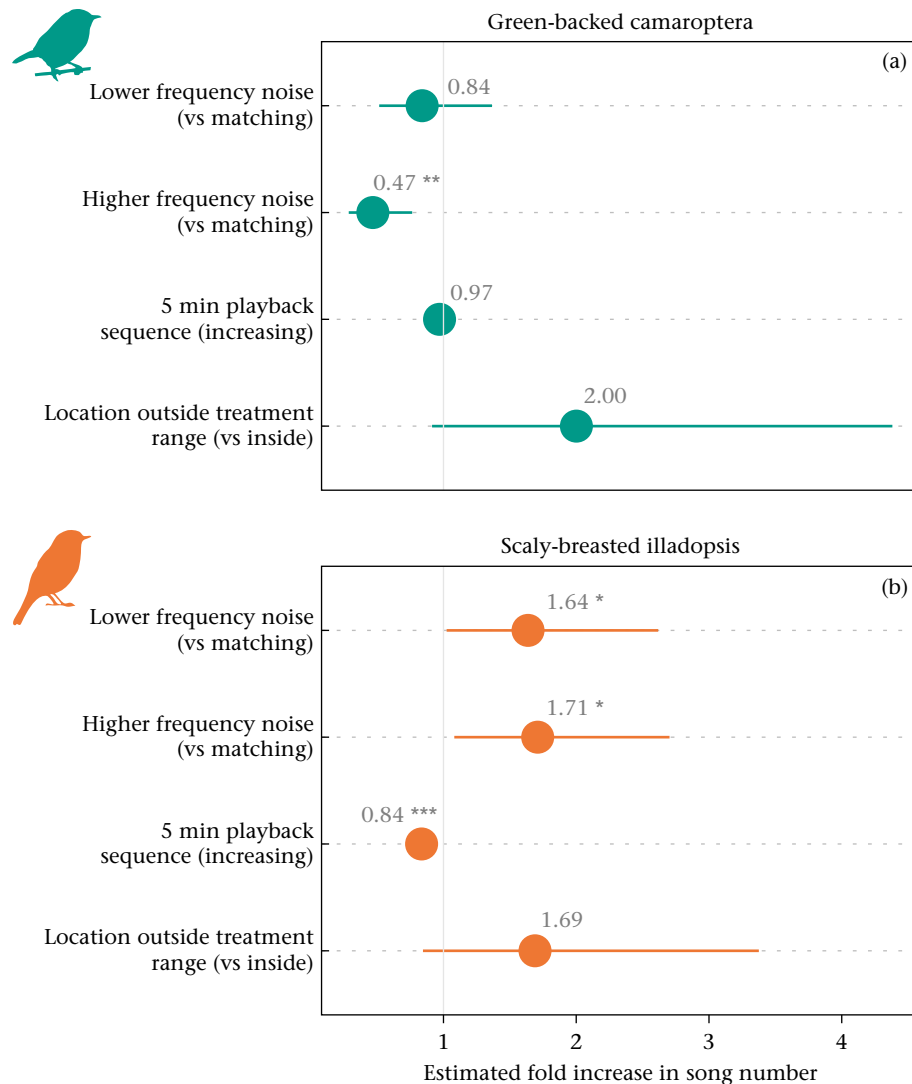


Figure 5. Odds ratios (ORs) of fixed effects estimates from the GLMMs predicting the difference in song rate in periods of lower and higher frequency noise compared to noise matching the species' song frequency with increasing experiment duration, and when the bird was outside the speaker range (compared to within the range of the speakers): (a) 22 green-backed camaroptera, *Camaroptera brachyura*; (b) 18 scaly-breasted illadopsis, *Illadopsis albipectus*. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Bars represent 95% confidence intervals. Full model output is given in Table 2.

vocally active throughout the day, when cicada vocalizations are common. Thus, although the higher frequency noise did not overlap with the birdsong frequency range, we speculate here that green-backed camaroptera could be responding to cicadas by reducing vocal activity. The higher frequency noise we presented to scaly-breasted illadopsis had a narrow frequency range (2.85–3.45 kHz), and thus did not correspond to the sound produced by cicadas. Further studies examining the effect of cicada vocalizations on bird behaviour can provide more information on the acoustic community relationships in Kibale National Park.

The two tropical passerines we tested responded differently to introduced competing acoustic signals (white noise). While scaly-breasted illadopsis appeared to use both temporal and spectral avoidance to reduce competition for acoustic space, neither of these strategies was observed in green-backed camaroptera. In contrast, individuals of this species only reduced their singing rate in response to noise above their frequency range. Moreover, during continuous noise overlapping their song frequency, green-backed camaroptera raised their singing rate suggesting that they may be increasing signal redundancy and thus the chance it will reach the receiver. Our results illustrate the divergence of behavioural

response strategies for acoustic-space competition avoidance within tropical forest passerines, which may result from differences in the acoustic properties of their songs and those of other species in the community.

Author Contributions

A.S., E.S. and M.B. conceived and developed the idea of the study. M.B. obtained funding. A.S. and E.S. conducted playback experiments and acoustic analyses. A.S. conducted statistical analyses and wrote the first draft of the manuscript. All authors contributed to the interpretation of results and to revising the manuscript.

Data Availability

Data are available in the Supplementary material.

Declaration of Interest

The authors declare that they have no competing interests.

Acknowledgments

We thank the personnel at the Makerere University Biological Field Station in Kanyawara for enabling us to work in Kibale National Park. Special thanks to Swaibu Katusabe and Perez Rukiri for their invaluable assistance in the field. We also thank Chris Sayers and Chris Sloan for permission to use their photographs of the birds. This study was supported by the National Science Centre, Poland (grant number 2019/35/D/NZ8/04416).

Supplementary Material

Supplementary material associated with this article is available in the online version at <https://doi.org/10.1016/j.anbehav.2024.01.006>.

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Appendix

Table A1
Playback order combinations

| Playback order | Green-backed camaroptera (N) | Scaly-breasted illadopsis (N) |
|---------------------------|------------------------------|-------------------------------|
| Lower – matching – higher | 4 | 3 |
| Lower – higher – matching | 3 | 3 |
| Matching – lower – higher | 4 | 3 |
| Matching – higher – lower | 4 | 2 |
| Higher – lower – matching | 4 | 4 |
| Higher – matching – lower | 3 | 3 |

Order combinations of frequency noise bands played when testing for spectral avoidance in green-backed camaroptera and scaly-breasted illadopsis, and the numbers of birds tested with each sequence combination.

Table A2
Comparisons between the two experiments of the species' song rate during playback of matching frequency noise

| | Coefficients | Estimate | SE | Z | P |
|---------------------------|-------------------------------|----------|-------|--------|---------|
| Green-backed camaroptera | Intercept | 2.470 | 0.290 | 8.530 | < 0.001 |
| | Experiment (continuous noise) | 0.467 | 0.258 | 1.813 | 0.070 |
| | Sequence | 0.027 | 0.034 | 0.785 | 0.432 |
| Scaly-breasted illadopsis | Intercept | 3.578 | 0.432 | 8.279 | <0.001 |
| | Experiment (continuous noise) | -0.104 | 0.558 | -0.189 | 0.85 |
| | Sequence | -0.226 | 0.041 | -5.581 | <0.001 |

GLMMs examining the effects of white noise playback matching the species' song frequency and sequence of the 5 min playback interval on the number of songs produced by green-backed camaroptera, *Camaroptera brachyura* (20 exposed to noise and silence and 22 exposed to continuous noise of varying frequency) and scaly-breasted illadopsis, *Illadopsis albipectus* (20 exposed to noise and silence and 18 exposed to continuous noise of varying frequency).

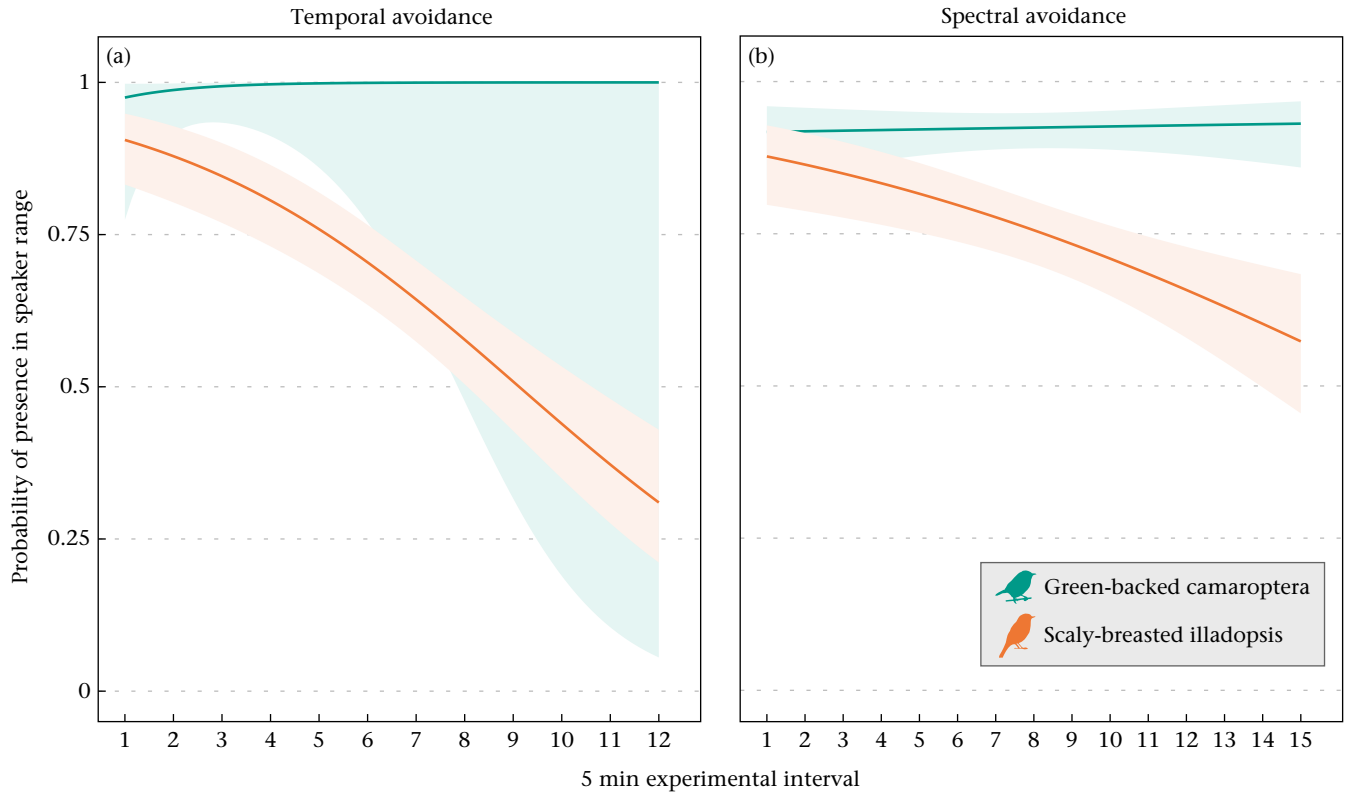


Figure A1. Results of the logistic regression testing the probability of study species remaining in the speaker range during the 5 min playback treatments. (a) Temporal avoidance experiment: 20 green-backed camaroptera, *Camaroptera brachyura* and 20 scaly-breasted illadopsis, *Illadopsis albipectus*; (b) spectral avoidance experiment: 22 green-backed camaroptera and 18 scaly-breasted illadopsis.