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Rainforest birds avoid biotic signal masking only in cases of high acoustic saturation

Laura Marie Berman^{1,2} · Wei Xuan Tan¹ · Ulmar Grafe³ · Frank Rheindt¹

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Abstract

Acoustic signaling among birds is central to intra-species communication, courtship, and reproductive success, and so habitat suitability is partially dependent upon the availability of a suitable acoustic niche. It is well documented that birds may modify their vocal behavior to avoid overlap with anthropogenic noise pollution, but responses to biotic signal making are less well understood. This study uses more than 50,000 h of audio recorded in tropical forest, and machine learning methods for the detection of the vocalizations of nine species of bird and tymbalizations of three species of cicada to examine patterns of signal masking and co-chorusing avoidance among species pairs. Among these focal species, no bird avoided co-chorusing with any other bird. Birds avoided co-chorusing with cicadas only and always when (1) the bird vocalized in a frequency band completely overlapped by the cicada tymbalization, and (2) the cicada tymbalization saturated the majority of that frequency band. These results indicate that avian behavioral modifications in response to biotic noise in longstanding species communities is similar to behavioral modifications observed in populations subjected to high levels of anthropogenic noise pollution—in all cases overlap avoidance is species-specific and dependent upon both frequency and intensity.

Keywords Bioacoustics · Signal masking · Machine learning · Tropical ecology

Zusammenfassung

Regenwaldvögel vermeiden biotische Signalmaskierung nur bei hoher akustischer Sättigung

Akustische Signalübertragung zwischen Vögeln ist von zentraler Bedeutung für die Kommunikation innerhalb der Art, die Balz und den Fortpflanzungserfolg. Daher hängt die Eignung eines Lebensraums zumindest teilweise von der Verfügbarkeit geeigneter akustischer Nischen ab. Es ist wohl bekannt, dass Vögel ihr Stimmverhalten verändern können, um Überschneidungen mit anthropogener Lärmbelästigung zu vermeiden. Ihre Reaktionen auf Signalmaskierung seitens biotischer Quellen sind jedoch weniger gut verstanden. Diese Studie basiert auf 50.000 Stunden von Audio-Material, welches in tropischen Wäldern aufgenommen wurde, sowie auf Methoden des maschinellen Lernens zur Erkennung der Lautäußerungen von neun Vogelarten und der Timbalisationen von drei Zikadenarten, um Muster der Signalmaskierung und der Vermeidung des simultanen Vokalisierens zwischen Artenpaaren zu untersuchen. Unter den Schwerpunktarten vermied keiner der Vögel simultanes Vokalisieren mit einer anderen Vogelart. Vögel vermieden simultanes Vokalisieren mit Zikaden immer nur dann, wenn (1) das Frequenzband der Vogelstimme ganz mit dem der Zikaden-Timbalisation überlappte, und wenn (2) die Zikaden-Timbalisation den Großteil dieses Frequenzbands sättigte. Diese Ergebnisse deuten darauf hin, dass Verhaltensveränderungen in Vögeln als Reaktion auf biotischen Lärm in langjährigen Artengemeinschaften denjenigen Verhaltensveränderungen ähneln, die in Populationen beobachtet werden, welche in einem hohen Ausmaß anthropogener

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✉ Frank Rheindt
dbsrfe@nus.edu.sg

¹ Department of Biological Sciences, National University of Singapore, Singapore, Singapore

² Yale-NUS College, Singapore, Singapore

³ Universiti Brunei Darussalam, Gadong, Brunei

Lärmbelästigung ausgesetzt sind – in all diesen Fällen ist die Vermeidung von Überschneidungen artspezifisch und hängt von Frequenz und Intensität ab.

Introduction

Communication is an essential aspect of animal ecology. Many taxa, including insects, mammals, and birds, use acoustic signals for intraspecific communication. Rainforest soundscapes have been compared to musical compositions because of the way each species fills a particular acoustic niche (Krause 1993). Each species typically has a specific frequency range in which it vocalizes and a particular time of day when it is most active, with minimal overlap with other species in the ecosystem. For example, birds which are vocally active at the same time of day, such as during the dawn chorus, tend to be more vocally distinct from one another (Luther 2009), and crickets partition acoustic space to use non-overlapping frequencies (Schmidt et al. 2013). In most natural multi-species choruses, there is sufficient acoustic space that effective acoustic overlap is near zero (Jain et al. 2014). Saturating noise which drowns out vocalizations can alter animal behaviors, sometimes leading to smaller territory sizes (Brumm and Zollinger 2013), pushing populations into quieter habitats (Rheindt 2003), or pushing vocalizations to higher or lower frequencies (Brumm and Zollinger 2013) or to earlier or later times of day (Arroyo-Solís et al. 2013).

Bird song generally does not saturate acoustic space; the songs of most bird species are tonal and contain gaps between motifs (Catchpole and Slater 2003, Brumm and Zollinger 2013). In contrast, many species of cicada have atonal droning choruses (e.g. Sueur 2002) in which multiple males sing simultaneously and which can reach high sound pressure levels (Young 1981). Bornean cicadas are speciose (Duffels et al. 2007; Duffels and Trilar 2012; Gogala and Riede 1995; Kos and Gogala 2000; Prešern et al. 2004; Trilar 2006) and form a dominant component of the soundscape. These types of loud cicada drones can alter the calling behavior of birds (Hart et al. 2015; Stanley et al. 2016). Some birds will adjust their song frequency to avoid interfering insect noise (Kirschel et al. 2009). Yet the role of insect noise in the soundscape and its impact on the acoustic niches of other taxa remains understudied, and the tymbalizations and stridulations of most species remain undescribed (Do Nascimento et al. 2023).

According to the acoustic niche hypothesis, species coordinate their vocalizations to avoid overlap and fill vacant acoustic space. We hypothesize that in order for signal masking avoidance to occur, it is not enough for species to overlap in time, space, and frequency. It is also necessary for the vocalization of one species to saturate the shared acoustic

space. Saturating sounds are loud, long, and broadband, fully occupying a frequency band over a period of time. Sounds from things like traffic and waterfalls have high saturation. High acoustic saturation is characteristic for the choruses of many cicada species, which have been hypothesized to drown out bird songs in many rainforest environments (Hart et al. 2015). To test this hypothesis, we compared bird songs and cicada choruses at three Southeast Asian rainforest sites and measured the degree to which each species' vocalization saturates its utilized frequency band. Finally, we assessed patterns of co-chorusing among species pairs to determine whether patterns were consistent with a hypothesis of overlap avoidance, particularly avoidance of species with high acoustic saturation.

Methods

Study sites

Acoustic monitoring stations were established at three sites across two countries in the Sundaic region: Andulau Forest Reserve, Brunei (4.658328 N, 114.521659 E), Central Catchment Nature Reserve, Singapore (1.355488 N, 103.804549 E), and Dairy Farm Nature Park, Singapore (1.358419 N, 103.777492 E) (Fig. 1). Singapore and Brunei have similar climatic conditions and forest cover, but contain distinct communities of bird and cicada species. Including sites from both countries allowed for the analysis of a wider cohort of species while still ensuring that the soundscapes were similar enough to be comparable.

Audio data collection

Soundscapes were recorded continuously for more than 2 years at long-term recording stations at each of the three sites, totaling more than 50,000 h of recordings. One recorder was deployed at each site. In Brunei, data were collected continuously from March 2019 until May 2021 using a Song Meter SM4 Wildlife Audio Recorder (Wildlife Acoustics) with a 44 kHz sampling rate. At the two Singaporean sites, data were collected continuously from June 2020 until May 2022 using AudioMoths (Open Acoustic Devices) modified for long-term deployment with a 16 kHz sampling rate. A 16 kHz sampling rate can record frequencies as high as 8 kHz; while some birds and cicadas vocalize at frequencies higher than this, all of the bird songs of interest in this study fall within this range. All audio files were 30 min in duration, beginning on the hour or half-hour.

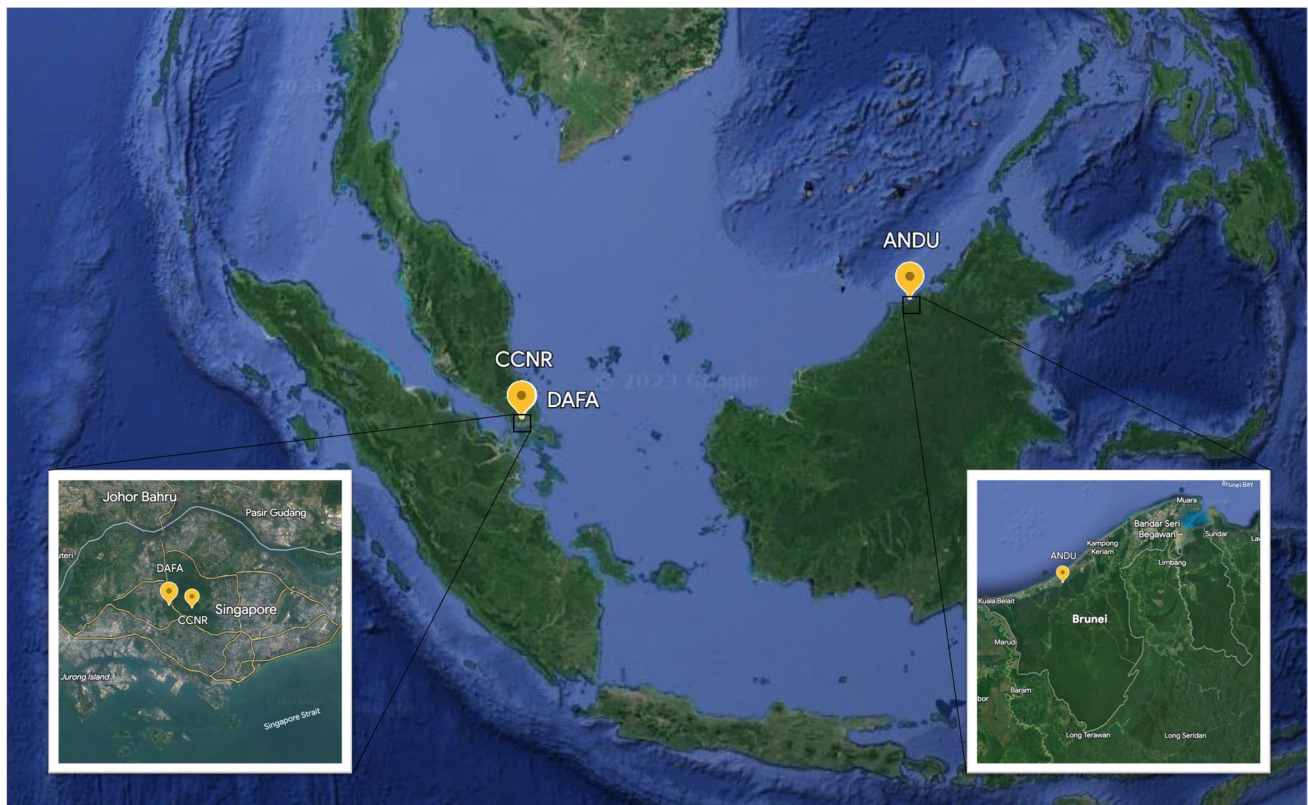


Fig. 1 Map of study sites. *ANDU* Andulau Forest Reserve, Brunei, *CCNR* Central Catchment Nature reserve, Singapore, *DAFA* Dairy Farm Nature Park, Singapore. Imagery from Google Earth

Focal species

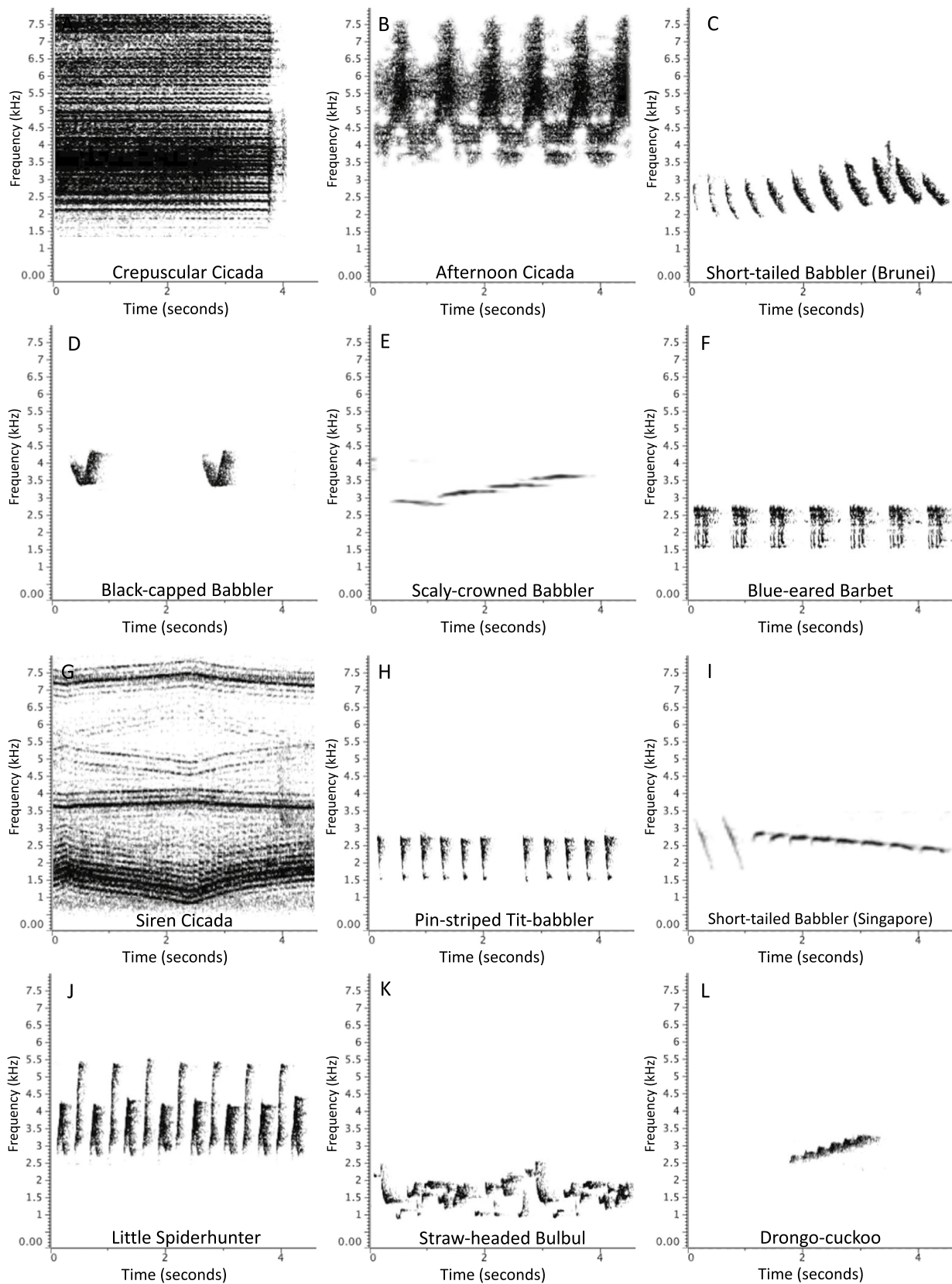
The species heard most often within the audio dataset were selected as focal species. Bird species included Scaly-crowned Babbler *Malacopteron cinereum*, Short-tailed Babbler *Pellorneum malaccensis*, Black-capped Babbler *Pellorneum capistratum*, Blue-eared Barbet *Psilopogon cyanotis*, Straw-headed Bulbul *Pycnonotus zeylanicus*, Pin-striped Tit-babbler *Mixornis gularis*, Drongo-cuckoo *Surniculus lugubris*, and Little Spiderhunter *Arachnothera longirostra*. Two different taxa of the Short-tailed Babbler *Pellorneum malaccensis* species complex occur in Singapore and Brunei, with distinct song types. Separate acoustic classifiers were made for these two taxa. Some common bird species with complex vocalizations which are challenging to classify conclusively (e.g. Greater Racket-tailed Drongo) were omitted from consideration. Not all species are heard at all sampling sites.

Cicadas in the Sundaic region are speciose and incompletely studied, with the tymbalizations of many species still undescribed, so unofficial monikers have been assigned to the three focal cicada species. The cicada with the pulsing drone is referred to as the ‘afternoon cicada’ because it is heard throughout the afternoon in Andulau Forest. The

monotonous drone with dense harmonics is called the ‘crepuscular cicada’ because it is heard at dawn and dusk in Andulau. And the drone shifting from high-to-low-to-high frequency, which sounds reminiscent of a siren, is referred to here as the ‘siren cicada’. Representative spectrograms of each species’ vocalization can be seen in Fig. 2 and audio recordings can be found in the supplementary materials. The afternoon and crepuscular cicadas here could potentially be the same still undescribed species referred to as ‘Morning Fanfare’ and ‘Riah Riah’ in Gogala and Riede 1995. The afternoon and crepuscular cicadas are heard only in Brunei, and the siren cicada is heard only in Singapore.

Machine learning

Species-specific classifiers were developed for nine species of bird and three species of cicada using the machine learning clustering software Kaleidoscope Pro 5.4.3 (Wildlife Acoustics, Maynard, MA, USA) to detect each time the songs of those 12 species appeared in the ~50,000 h dataset. A species classifier is a machine learning algorithm trained to detect and identify a single species. To identify candidate focal species, a random selection of 1000 audio files from the dataset were manually listened to and a record was made



Brunei

Singapore

Fig. 2 Representative spectrograms of the focal species found in Brunei and Singapore. Species in panels A–F occur in Brunei. Species in panels G–L occur in Singapore. Spectrograms generated in Raven Pro 1.6.4 (Cornell lab of Ornithology, Ithaca, NY, USA)

of all species that could be positively identified within each file. The most common were selected as focal species.

Kaleidoscope Pro uses a two-step process that initially scans all recordings for sounds that match the general parameters of the target vocalization, before clustering those sounds. To identify appropriate signal parameters for each species, the calls from 10 unattenuated recordings of each species were characterized in Raven Pro 1.6.4 (Cornell lab of Ornithology, Ithaca, NY, USA) to find the minimum and maximum frequency, the minimum and maximum duration, and the maximum inter-syllable gap. To ensure that the broadest range of signals would be detected, absolute minimum and absolute maximum values were kept, values were not averaged. The signal parameters for all 12 species can be found in Table 1.

A training dataset was compiled for each species classifier. Training datasets were composed of vocalizations of the focal species, vocalizations from similar sounding species found at the study sites, and interfering background noise, using both recordings from the dataset and from the audio database xenocanto.org. Constructing the training datasets this way ensured that classifiers could distinguish between similar sounding species, and could accurately identify the target species under a wide range of conditions. The amount of training data of each type used for each species classifier is available in Table 1.

For each classifier all potential detections were manually verified up to the maximum distance from the cluster center to minimize false negatives while removing false positives. In Kaleidoscope Pro, detected sounds are assigned a value, the ‘distance from cluster center’, which describes how similar a sound is to the stereotypical vocalization that the classifier is trained to identify, where better matches are closer to the center, and poor matches are further. Including and verifying poor matches is particularly important for this study, since detecting instances of co-chorusing is central to the research question, and overlapped vocalizations are often further from the cluster center. To ensure that as few as possible of these overlapped vocalizations were missed, we set the ‘maximum distance from cluster center’ to its maximum value, which forces all detected sounds into the cluster analysis results, even if their similarity to the cluster center is not statistically significant. ‘All detected sounds’ means every sound in the 50,000 h dataset which falls within the general parameters of the species classifier, i.e. every sound falling within the correct frequency range and lasting an appropriate duration. Every one of these detections, from likely matches to extremely unlikely matches, was then manually verified as either a true detection or removed as a false positive.

The recall rate of each classifier was estimated by manually labeling the presence or absence of each focal species in 1320 audio files. The recall rate was the percentage of

manually labelled occurrences which were successfully detected by the species classifier.

Cases where cicada droning was so loud that overlapping bird song would be undetectable by even manual identification is one potential source of bias. Approximately 7% of afternoon cicada drones, and none of the crepuscular cicada drones or siren cicada drones were loud enough to inhibit the manual detection of any birds that might be singing over them. These estimates were made manually by classifying 40 randomly selected cicada drones per species as either capable or not capable of inhibiting manual identification of overlapping birdsong.

Measuring acoustic saturation

For each species, spectrograms were generated for five bouts, cropped to that species’ respective frequency band, and contrast was adjusted so that the target sound displayed as pure black with a pure white background. The number of black pixels was divided by the total number of pixels and averaged across the five bouts to find the average acoustic saturation of each species (Fig. 3). To avoid ambiguity when distinguishing between the focal species’ vocalizations and background noise, only clear, unattenuated recordings with minimal background noise were used for acoustic saturation measurements. Harmonics were considered to be part of the vocalizations. A bout typically consists of a specific motif repeated at regular intervals. All focal species had regular inter-motif gaps with the exception of crepuscular cicadas and afternoon cicadas, which sang long continuous drones. For these two species, individual drones were considered to be bouts. The duration of a bout was considered to extend beyond the final motif by the average duration of one inter-motif gap. Including this ‘white space’ at the end gives a more accurate average acoustic saturation by including an equal number of motifs and inter-motif gaps. Tonal sounds with long inter-motif gaps typically have low acoustic saturation, while atonal sounds with short gaps tend to have high acoustic saturation.

Frequency range and overlap

The frequency range of each species is bounded by the absolute minimum and absolute maximum frequency of the species’ vocalization across ten randomly selected 30-min audio files from the audio dataset which contained clear (not attenuated) bouts of song. Maximums were rounded up to the nearest 100 Hz, and minimums were rounded down. Low frequencies below 1000 Hz were rounded down to the nearest 10 Hz. Absolute max and min frequencies were used to ensure no parts of the vocalizations were lost, because Kaleidoscope Pro only acknowledges sound within the designated frequency band. The frequency range of each species can

Table 1 Acoustic saturation, signal parameters, training data, number of detections, and recall rate for each of the 12 taxa

Species	Site	Average acoustic saturation	Signal parameters			Training data				Detections				Recall rate		
			Frequency range	Duration	Inter-syllable Gap	FFT Window	Files from study site		Files from xenocanto		Brunei	Singapore				
							Focal	Non-focal	Total	Focal		Non-focal	Total		Central	Dairy farm
Afternoon Cicada	Brunei	0.837	3000–7000 Hz	10–50 s	0 s	21.33 ms	24	199	223	0	25	25	3314	0	0	33%
Crepuscular Cicada	Brunei	0.642	2000–7000 Hz	10–50 s	0 s	21.33 ms	8	215	223	0	25	25	3433	0	0	75%
Black-capped Babbler	Brunei	0.068	3100–4300 Hz	0.5–0.6 s	0 s	5.33 ms	39	39	78	23	241	264	7102	0	0	43%
Blue-eared Barbet	Brunei	0.179	1400–2700 Hz	0.2–0.3 s	0.08 s	5.33 ms	12	381	393	35	3013	3048	9504	0	0	53%
Scaly-crowned Babbler	Brunei	0.011	2500–4000 Hz	2.5–4.0 s	0.2 s	5.33 ms	15	196	211	10	614	624	2846	0	0	64%
Short-tailed Babbler (Brunei)	Brunei	0.062	1700–3600 Hz	2.0–4.0 s	0.3 s	5.33 ms	22	105	127	14	1797	1811	15,922	0	0	74%
Siren Cicada	Singapore	0.28	690–3000 Hz	9–15 s	0.24 s	5.33 ms	19	72	91	0	130	130	0	8009	2907	85%
Little Spiderhunter	Singapore	0.12	2400–5800 Hz	3.0–8.0 s	0.23 s	5.33 ms	36	316	352	33	1033	1066	0	1	15,629	55%
Pin-striped Tit-babbler	Singapore	0.067	1400–3000 Hz	1.0–3.0 s	0.4 s	5.33 ms	57	196	253	0	0	0	0	4041	2565	47%
Short-tailed Babbler (Singapore)	Singapore	0.028	1500–3600 Hz	1.8–8.3 s	0.4 s	5.33 ms	8	346	354	15	2612	2627	0	9453	144	80%
Drongo-cuckoo	Singapore	0.071	2200–3400 Hz	1.5–2.0 s	0.2 s	5.33 ms	9	4	13	6	0	6	0	449	6926	59%
Straw-headed Bulbul	Singapore	0.044	720–2700 Hz	2.0–8.0 s	0.38 s	5.33 ms	31	321	352	0	2109	2109	0	7	432	79%

Signal parameters are the parameters used for the initial signal detection scan in Kaleidoscope Pro. Kaleidoscope will detect sounds as potential matches if they fall within the frequency range and last an appropriate duration. Detections are the number of manually verified true positive detections. Sites with fewer than 200 detections of a species' vocalization were excluded from statistical analysis due to low sample size. Recall rate is the estimated percentage of vocalizations in the 50,000 h dataset that were successfully detected by the classifier

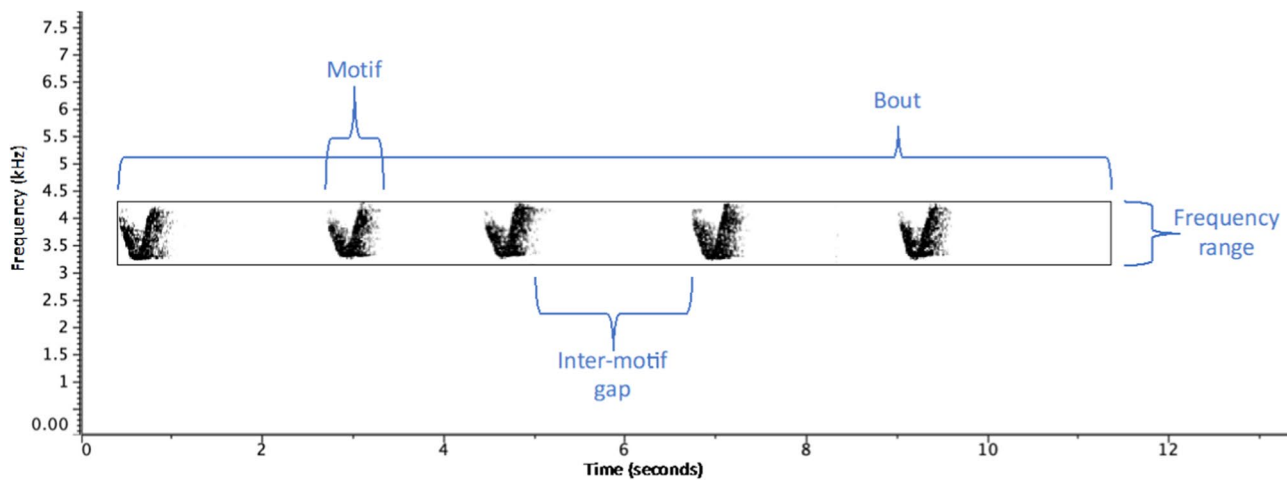


Fig. 3 Example of a spectrogram used to measure the acoustic saturation of Black-capped Babblers. Within the demarcated black box, which extends for the duration of the bout, from the lower to the upper bound of the frequency range, 14,170 pixels are occupied by the vocalization (black pixels) out of 208,392 total pixels = 6.8% sat-

uration. Black-capped Babblers sing a tonal motif with a long inter-motif gap, saturating only 6.8% of their frequency range over the course of a bout. Black-capped Babbler bouts typically last longer than five motifs. Spectrogram generated in Raven Pro 1.6.4 (Cornell lab of Ornithology, Ithaca, NY, USA)

be found in Table 1. Frequency overlap is simply whether the frequency ranges of two species overlap. Complete frequency overlap is when one species' frequency range falls entirely within the frequency range of another species. Partial overlap is when only part of a species' frequency range is overlapped by another species.

Testing for signal masking avoidance

A Cochran–Mantel–Haenszel test (Cochran 1954, Mantel and Haenszel 1959) was used to determine whether signal masking avoidance might exist between species pairs. More specifically, a Cochran–Mantel–Haenszel test is a type of time-stratified chi-squared test which was used to determine whether species pairs which occurred at the same site, were vocally active at the same time of day, and used overlapping frequency bands in their songs were less likely to sing together simultaneously than was predicted under the assumptions of independence. For example, if both Black-capped Babblers and afternoon cicadas often sing at 8:50 am in Andulau Forest Reserve, are Black-capped Babblers less likely to be heard at 8:50 am on days when afternoon cicadas are singing at 8:50 am? The time stratification of the Cochran–Mantel–Haenszel test ensures that the results are not biased by the diel niche of each species. The full 50,000 h dataset was stratified into 10-min intervals, and during each 10-min audio clip a species' vocalization was either detected or not detected. Species pairs were considered to be co-chorusing if both occurred within the same 10-min clip. A 10-min interval size was chosen because bouts of cicada droning typically lasted at least 10 min. A common odds ratio of less than one and a p value of less

than 0.05 indicates that the species pair was observed co-chorusing significantly less than predicted by independence. Species pair comparisons were limited to those with at least 200 detected vocalizations per species per site (Table 1), and those with at least partially overlapping active periods during the day (Fig. 4), to ensure sufficient sample size for statistical analysis.

Results

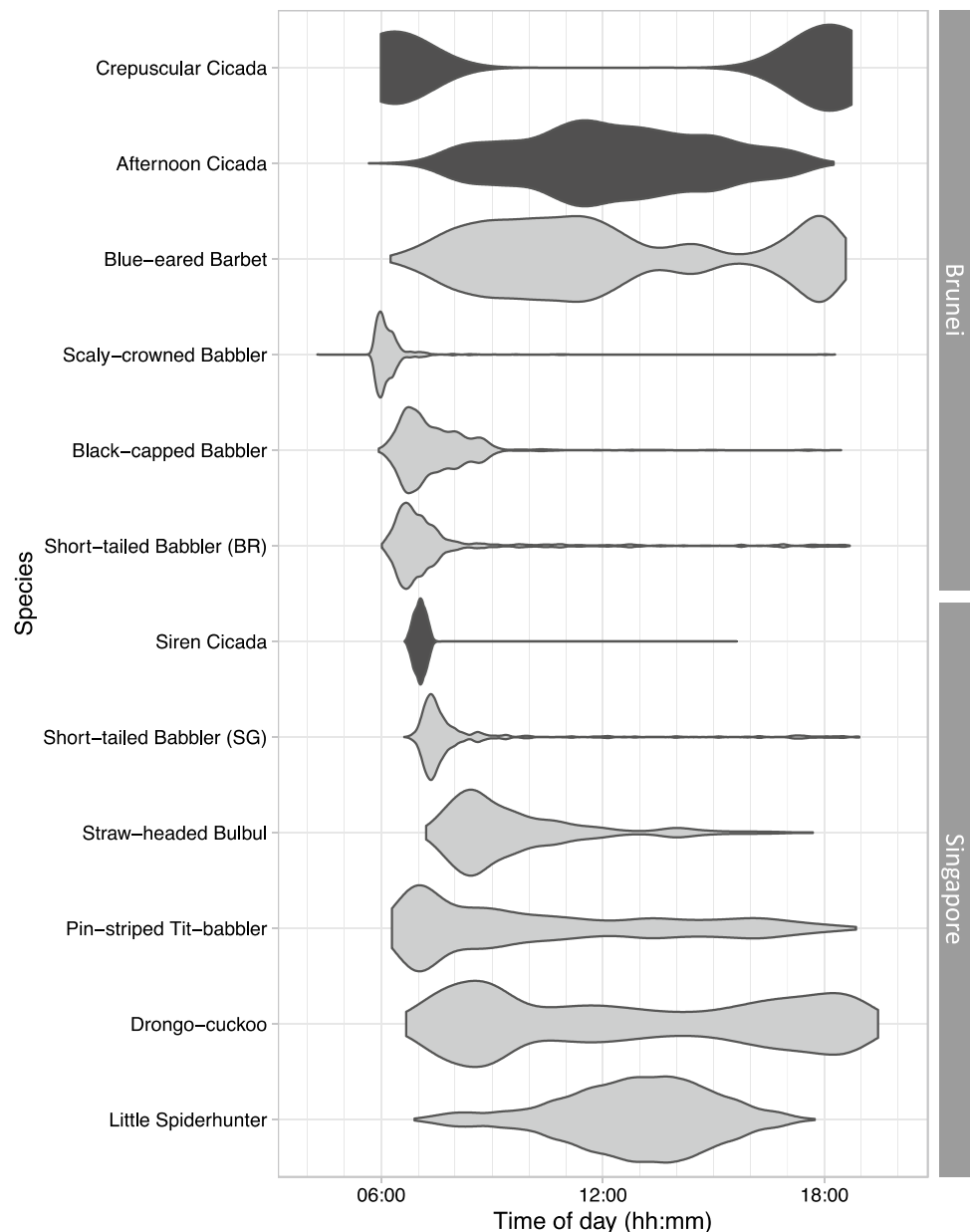
Acoustic saturation

Cicada drones saturated more of the acoustic space within their respective frequency bands as compared to bird song (Fig. 5). The afternoon cicada saturated 84% of its frequency band, the crepuscular cicada saturated 64%, and the siren cicada saturated 28%, while bird songs saturated only 4–18% of their frequency bands.

Signal masking avoidance

Among the 15 cicada-versus-bird species pairs, co-chorusing occurred significantly less often than predicted by independence only in three cases: Scaly-crowned Babblers v. crepuscular cicadas, Black-capped Babblers v. crepuscular cicadas, and Black-capped Babblers v. afternoon cicadas (Fig. 6, Table 2). Co-chorusing avoidance only occurred when a species with high acoustic saturation completely overlapped the frequency band of the other species (Table 2).

Fig. 4 Species' vocal activity by time of day. Violin plot height is proportional to the density of detected vocalizations across time, where the tallest point on the plot is the time of day when that species is most vocally active, scaled so that the maximum height of all plots are equal (geom_violin(scale="width")). Black: cicadas. Grey: birds. Figure generated in R using packages ggplot2 (Wickham 2016) and lubridate (Grolemund and Wickham 2011)



Discussion

Overlap avoidance from cicadas with high acoustic saturation

Birds were observed to sing significantly less, in a pattern consistent with signal masking avoidance, only in cases where (a) the masking song completely overlapped the frequency band of the bird song, and (b) where the masking song saturated the majority of the acoustic space (Table 2). Among the 15 species pairs assessed, every time these two conditions were met there was significant avoidance of song overlap. In cases with only partial frequency overlap or low acoustic saturation there was no avoidance of overlap

(Table 2). Black-capped Babblers and Scaly-crowned Babblers are significantly less likely to be heard singing during their preferred time window on days when crepuscular cicadas or afternoon cicadas are also singing.

Studies analyzing temporal acoustic niche partitioning generally frame the research question in one of two ways. Either they assess whether species singing in the same chorus make fine-scale adjustments to the timing of their song to place their vocalizations in the silent gaps between motifs within the bouts of co-chorusing individuals (Masco et al. 2016), or, rather than fine-scale temporal coordination, they look at broader-scale co-chorusing avoidance among species occupying competing acoustic niches. There is bountiful evidence of fine-scale temporal coordination among

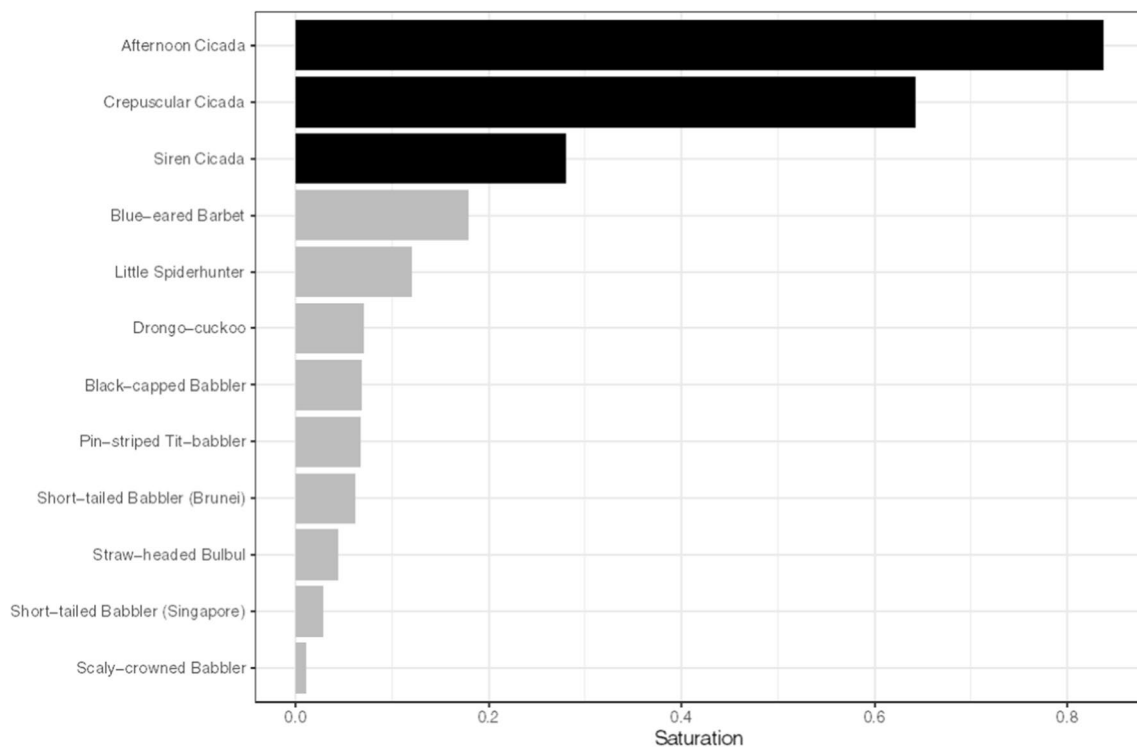


Fig. 5 Average acoustic saturation by species. Black: cicadas. Grey: birds. Acoustic saturation is a measure of the average proportion of acoustic space occupied by the vocalization of a species within its utilized frequency band across the duration of a bout of song

co-chorusing birds (Hart et al. 2021; Yang et al. 2014; Ficken et al. 1974; Cody & Brown 1969), but even birds occupying highly similar acoustic niches generally do not avoid co-chorusing (Kleyn et al. 2021), as evidenced by the existence of the dawn chorus. In contrast, birds have been found to avoid co-chorusing with certain species of cicadas, as the results of this study show. In Costa Rica and Panama, bird species using competing frequency bands will stop singing with the onset of broadband droning *Zammara smaragdina* cicada choruses (Hart et al. 2015; Stanley et al. 2016). In other cases, birds have been found to adjust the frequency of their vocalizations to avoid overlap with high intensity insect noise (Kirschel et al. 2009). Birds' response to high-saturation, broadband cicada droning is similar to the adaptive responses recorded at sites with anthropogenic noise pollution. In both cases the response is frequency-specific, and dependent upon the high intensity and saturation of the interfering noise. Birds with low-frequency vocalizations can be excluded from environments with low-frequency noise pollution (Francis et al. 2011). Signals are more effectively masked by noise energy in the spectral region of the signal, and detection thresholds increase as noise level increases (Lohr et al. 2003).

Not all cicadas have tymbalizations which saturate a frequency band. The siren cicada saturated on average only 28% of its frequency band during any given bout, and no birds avoided co-chorusing with it. Whether or not cicada droning could exclude birdsong may depend on both the species-specific tymbalization and the population density. Cicadas form single-species choruses of many males singing simultaneously, and a higher population density may result in an overall more saturated broadband drone. A single tymbalization from a siren cicada lasts about 12 s before lapsing into silence (see supplementary materials for example audio recordings), but when multiple individuals call together the overall drone can last much longer. Siren cicadas do not synchronize with one another when chorusing, and their tymbalizations fluctuate in frequency high-to-low-to-high, so that when one individual is singing the high part of the motif, another individual might be singing the low part. This unsynchronized chorusing means that acoustic saturation can differ depending on the number of individuals singing. While at the study site this species saturates on average 28% of its frequency band while vocally active, it may be the case that at higher population densities acoustic saturation increases.

Fig. 6 Visualization of Cochran–Mantel–Haenszel test for overlap avoidance. Co-chorusing patterns of the three species pairs with significant overlap avoidance. **A** Black-capped Babbler and afternoon cicada, **B** Scaly-crowned Babbler and crepuscular cicada, **C** Black-capped Babbler and crepuscular cicada. Light blue colour indicates the few instances when birds were heard singing over cicadas. The Cochran–Mantel–Haenszel test creates a contingency table for each 10-min vertical column, and performs chi-squared tests for each 10-min stratification. This allows us to estimate how often two species would be expected to co-chorus while accounting for the diel niche of each species, and whether the observed number of co-chorusing events differ significantly from those predicted under conditions of independence



Conclusion

Much research has been carried out on the effects of anthropogenic noise pollution on the vocal behavior of birds, while comparatively little has been published on how the avian

community reacts to high saturation biotic noise. The soundscape is an important aspect of habitats and ecosystems, and understanding the dynamics of species acoustic interactions allows us to more comprehensively assess the characteristics that make particular habitats suitable for specific species.

Table 2 Instances of co-chorusing among species pairs

Species 1	Species 2	Site	Frequency overlap	Co-chorusing		P-value	Common odds ratio
				Expected	Observed		
Afternoon Cicada (84% saturation)	Black-capped Babbler	ANDU	Complete	12.0	1	1.69E−03	0.08
	Blue-eared Barbet	ANDU	None	37.9	41	0.66	1.09
	Scaly-crowned Babbler	ANDU	Partial	1.3	1	0.78	0.75
	Short-tailed Babbler (BR)	ANDU	Partial	46.5	51	0.64	1.08
Crepuscular Cicada (64% saturation)	Black-capped Babbler	ANDU	Complete	30.0	19	0.03	0.57
	Blue-eared Barbet	ANDU	Partial	22.3	17	0.26	0.72
	Scaly-crowned Babbler	ANDU	Complete	54.2	20	7.53E−08	0.3
	Short-tailed Babbler (BR)	ANDU	Partial	119.2	130	0.25	1.14
Siren Cicada (28% saturation)	Little Spiderhunter	DAFA	Partial	11.7	31	2.87E−10	4.89
	Pin-striped Tit-babbler	CCNR	Complete	125.5	162	1.87E−05	1.61
	Pin-striped Tit-babbler	DAFA	Complete	50.2	56	0.37	1.17
	Straw-headed Bulbul	DAFA	Complete	0.3	3	1.62E−05	11.6
	Short-tailed Babbler (SG)	CCNR	Partial	145.2	135	0.27	0.88
	Drongo-cuckoo	CCNR	Partial	0.3	0	0.55	0
	Drongo-cuckoo	DAFA	Partial	7.3	9	0.61	1.34

Cochran–Mantel–Haenszel test: a common odds ratio of less than one and a p value of less than 0.05 indicates that the species pair co-chorused significantly less than expected under conditions of independence (significant pairs shown in bold). Avoidance occurred if and only if frequency overlap was complete and acoustic saturation was high. Co-chorusing (expected): the number of times the species pair would be expected to co-chorus under conditions of independence, after accounting for the diel niche of each species. Co-chorusing (observed): the number of times the species pair was heard co-chorusing. *ANDU* Andulau Forest Reserve, Brunei. *DAFA* Dairy Farm Nature Park, Singapore. *CCNR* Central Catchment Nature Reserve, Singapore

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Data availability Original audio files are archived in the Fonoteca Neotropical Jacques Viellard (FNJV) Audiovisual Collection [<https://www2.ib.unicamp.br/fnjv/>].

Declarations Ethical approval

Audio equipment was deployed under Singapore National Parks Board permit number NP/RP19-113. All work done in association with this manuscript complies with the current laws of the countries in which it was performed.

Conflict of interest The authors declare that they have no competing interests to disclose.

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