

Acoustic phenology among tropical resident birds differs between native forest species and parkland colonizer species

Laura Berman¹, Wei Xuan Tan¹, Ulmar Grafe², and Frank Rheindt¹

¹National University of Singapore

²Universiti Brunei Darussalam

March 31, 2024

Abstract

Most birds are characterized by a seasonal phenology closely adapted to local climatic conditions, even in tropical habitats where climatic seasonality is slight. In order to better understand the phenologies of resident tropical birds, and how phenology may differ among species at the same site, we used ~70,000 hours of audio recordings collected continuously for two years at four recording stations in Singapore and nine custom-made machine learning classifiers to determine the vocal phenology of a panel of nine resident bird species. We detected distinct seasonality in vocal activity in some species but not others. Native forest species sang seasonally. In contrast, species which have only had breeding populations in Singapore for the last few decades exhibited seemingly aseasonal or unpredictable song activity throughout the year. Urbanization and habitat modification over the last 200 years have altered the composition of species in Singapore, which appears to have influenced phenological dynamics in the avian community. It is unclear what is driving the differences in phenology between these two groups of species, but it may be due to either differences in seasonal availability of preferred foods, or newly established populations may require decades to adjust to the local phenology. Our results highlight the ways that anthropogenic habitat modification may disrupt phenological cycles in tropical regions in addition to altering the species community.

INTRODUCTION

Phenology, the timing of biological events within seasonal cycles, is a vital aspect of the life history of all species (Schwartz 2013). Knowledge of a species' phenology is necessary to fully understand its role within the ecosystem. In the case of endangered species, information on phenology can help target conservation efforts during the season when potential payoff is highest (e.g. Perkins et al. 2013). Shifts in phenology are among the most widely documented biotic responses to global climate change (Scheffers et al. 2016, Oliver et al. 2018), often leading to ecologically disruptive asynchronies. Phenology is central to both understanding the ecology of ecosystems and to the conservation of species. Reproductive phenology is a basic aspect of birds' life history which is well studied in temperate regions, but is a comparatively younger field of research in the tropics (Abernethy 2018). Phenological studies of Southeast Asian birds are especially scarce (Sodhi 2002). The paucity of studies on tropical seasonality is partially due to historical inequities in the focus of scientific research, and partially due to the comparative difficulty – phenological patterns in tropical regions are often less obvious than in temperate ones (Stutchbury and Morton 2001).

While reproductive seasonality among birds is generally understood to be the norm, even near the equator (Baker 1939, Snow and Snow 1964, Bell 1982), seasonal fluctuations in food supply are less pronounced in equatorial regions, leading to greater variability among species in the timing of the breeding season (Stutchbury and Morton 2001, Stouffer et al. 2013). Individual species might breed outside the typical season due to competition for nesting sites (Steward et al. 2013, Sadanandan et al. 2023), particular diets (Ralph and Fancy 1994), or taxon-specific requirements (Serle 1981). Phenology can sometimes shift dramatically across small geographic scales due to differences in climate (Wrege and Emlen 1991, Thomas

et al 2001, Moore et al. 2005). As anthropogenic climate change intensifies, it is becoming increasingly important to understand phenological cycles of biota in the tropics, where biodiversity is greatest and under greatest threat, how those cycles are linked to local climates, and how they might be disrupted as the climate changes. Moreover, some avian clades may be more resilient to warming than others (Pollock et al 2021). More detailed research is needed to understand the phenology of tropical birds on a species-specific level and at a detailed geographical scale.

Long term soundscape recordings can be used to determine the breeding phenology of birds (Brumm and Zollinger 2013, Jahn et al. 2017, Pérez-Granados and Schuchmann 2020). New bioacoustic technologies have made it possible to explore questions which were difficult or impossible to address with traditional methods (Pijanowski et al. 2011, Shonfield and Bayne 2017). Autonomous recording units (ARUs), which can be deployed outdoors to record long-term continuous soundscape data, have become increasingly reliable, user friendly, and inexpensive in recent years, making the widespread use of this technology more feasible for large scale projects and more common as an aspect of long-term ecological monitoring regimens (Hill et al. 2018, Manzano-Rubio et al. 2022, Bota et al. 2023). Long-term autonomous bioacoustic monitoring has many advantages over traditional survey methods: it is less labor intensive, less expensive, less prone to observer bias, can be used at difficult-to-access locations, and creates an archival record which enables the comparison of vocalizations and soundscapes across time (Frommolt et al. 2008, Borker et al. 2015, Shonfield and Bayne 2017). While acoustic monitoring is becoming more common, continuous multi-year datasets are still rare. This study makes use of an exceptionally large and complete soundscape dataset: two full years of continuous 24/7 soundscape recordings from four ARUs deployed in the forests of Singapore, a small Southeast Asian country only 1° north of the equator.

Recent advances in machine learning technology have made it possible to efficiently process the terabytes of data produced by each monitoring station over the years (Stowell et al. 2019). Long term acoustic monitoring in combination with machine learning analysis has a wide utility in ecological research: it can be used for assessment of population dynamics, activity patterns, and human impacts on a site over time, for rapid site inventories, to detect and map the habitats of rare and endangered species, and to determine the phenological cycles of individual species (Bardeli et al. 2010, Shonfield and Bayne 2017, Deichmann et al. 2018). Software like Kaleidoscope Pro (Wildlife Acoustics) and BirdNET (Cornell Lab of Ornithology) are able to automatically detect and identify species' vocalizations with a high degree of accuracy (Manzano-Rubio et al. 2022) and can be trained to identify new species.

The objectives of this study were to elucidate the species-specific breeding seasons of some of the birds of Singapore. To meet this objective, we used two years of continuous soundscape recordings and nine tailor-made species-specific machine learning classifiers to determine the seasonal vocal activity of nine focal species. There were two emergent properties in the preliminary results which warranted further analysis. First, several species did not appear to follow any seasonal pattern at all in their vocal activity. To quantitatively measure this pattern, we developed a novel seasonality index which measures the extent to which vocal activity is seasonal or aseasonal. While a number of excellent R functions exist for detecting and extracting the seasonal component of a trend (e.g. decompose), none measure the strength of seasonality. Our novel seasonality index fills this gap. Second, the least seasonal species appeared to be those which had not historically occurred at the study site. To quantitatively assess this apparent pattern, focal species were categorized *post-hoc* into native forest species versus parkland colonizer species and the degree of seasonality of each species' vocal activity was measured.

METHODS

Study area

Data were collected in Singapore, a small Southeast Asian island nation (1.3°N, 103.7°E; 734 km²) located within the Sundaic biogeographic region close to the equator with a tropical rainforest climate. It is hot and rainy year-round. Climatic seasonality is weak, but on average it is slightly sunnier in February-March and rainier in November-December (Figure 1, Berman et al. 2023). Historically this island was dominated

by mixed dipterocarp everwet forest. Singapore, however, has undergone dramatic urbanization in the last 200 years: only 0.28% of its original primary forest cover remains (Yee et al. 2011) and about 30% of the native bird species have gone nationally extinct (Chisholm et al. 2016, Chisholm et al. 2023). Currently, 20% of the country's land cover is secondary forest (Yee et al. 2011), which ranges from native-dominated old secondary forest within nature reserves to open woodlands dominated by primarily exotic tree species.

While the urbanization of Singapore has led to the local extinction of many forest interior species, it has also led to the colonization of regionally local species adapted to more open habitat. The four recording stations in Singapore were in Sungei Buloh Wetland Reserve (1.441586 N, 103.735308 E), Dairy Farm Nature Park (1.358419 N, 103.777492 E), Central Catchment Nature Reserve (1.355488 N, 103.804549 E), and National University of Singapore Campus (1.295020 N, 103.779385 E). These recording stations were 3-10 km apart from one another. All recorders were placed in mixed dipterocarp tropical rainforest habitat. The recording stations in Central Catchment Nature Reserve, Sungei Buloh Wetland Reserve and Dairy Farm Nature Park were all in mature secondary mixed dipterocarp tropical rainforest, while the recording station on the National University of Singapore campus was located in early-stage successional forest. These four recording sites were close enough to one another, and located in sufficiently similar habitat, that we would not expect phenology to differ among them. Data from these four recording stations were amalgamated into a single dataset to maximize sample size for each species.

Hosted file

image1.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

Figure 1. Seasonal climate of Singapore. Data obtained from weatherspark.com.

Audio recordings

Audio data was collected continuously for two years at each recording station for a total of about 70,000 hours. Each audio file begins on the half hour and has a duration of 29 min 55 sec, with a 5 second rest period between files for data writing. The study period ran from June 2020 – May 2022. Data was recorded on AudioMoth acoustic recorders (Open Acoustic Devices) modified for long-term deployment: eight supplementary battery packs were wired in parallel to each AudioMoth, increasing the potential battery life eight-fold, and each unit was placed inside a custom-built waterproof 15x20x10 cm enclosure, with an aperture for the microphone protected by a waterproof acoustic membrane and a wire mesh. Units were deployed at shoulder height and attached to a tree via python lock. Units were checked once every 5 weeks to replace batteries, SD cards and desiccant, and to collect data. Every 5 weeks, units were given enough battery power and SD memory to collect data continuously for another 6 weeks, to provide a one-week buffer. AudioMoth units were set to collect data with a 16 kHz sampling rate, medium gain, and no subsampling or filtering. All recording units were deployed inside forest and at least 50 m from the nearest publicly accessible trail to minimize human disturbance.

Handling missing data

There were a few instances when recorder failure led to missing data, most notably in the first half of February 2022. Recorder failure was typically caused by low battery voltage and resulted in premature termination of recordings, i.e., files with a duration of less than 29 minutes and 55 seconds. A complete record of all dates and times with missing data can be found in the Supporting Information. When reporting number of vocalizations per hour or per month, the true recording duration was used as the denominator to account for missingness in the time series and variability in the duration of months. Hours with greater than 60% missingness were omitted from the time series.

Manual identification

Manual identification was used to identify candidate focal species and collect vocalizations to be used in

species classifiers. A random selection of 1,000 audio files from the complete audio dataset were manually assessed and a record was made of all species that could be positively identified within each file in order to determine which species were heard most often and would therefore make the best candidate focal species. Files with positive identifications were then used as part of the training datasets for the single species classifiers. These manual identifications were used again later in the workflow to measure the recall rate of the completed species classifiers.

Classifier training

After nine focal species had been identified, custom-made single-species classifiers were trained for each focal species using the machine learning clustering software Kaleidoscope Pro v 5.4.8 (Wildlife Acoustics). Each classifier was used to detect and identify vocalizations from one species. Kaleidoscope Pro uses a two-step process for species identification: scanning and clustering. During the scanning step, Kaleidoscope scans the dataset of audio files for sounds that match a set of signal parameters tuned to pick up the focal species. Those matching target sounds are extracted, and Kaleidoscope then clusters those sounds based on similarity, and those clusters can be trained to accurately place vocalizations from the focal species into one cluster, while noise and similar sounding species go in other clusters. Appropriate signal parameters were chosen by measuring the minimum frequency, maximum frequency, minimum motif duration, maximum motif duration, and maximum inter-syllable gap of five unattenuated recordings of each focal species. Unattenuated vocalizations were collected from among the site recordings and found during the manual identification step. Absolute minima and absolute maxima, rather than averages, were used to ensure the edges of detected vocalizations were not lost during the scanning step. Spectrogram measurements were taken in Raven Pro v 1.6.4 (Cornell Lab of Ornithology, Ithaca, NY, USA). Signal detection parameters for each species classifier can be found in Table 1.

Once appropriate signal parameters had been identified, a training dataset was compiled for each species. For each classifier, the training dataset contained a) examples of vocalizations from the focal species at the study site, b) randomly selected audio files from the study site which did not include vocalizations from the focal species to be used as negative examples, c) clean recordings of the focal species obtained from the online sound library Xeno-Canto (xeno-canto.org), and d) example audio recordings from the cohort of non-focal species which occur at the study site, also from Xeno-Canto. Setting up the training datasets this way ensured that there were clear examples of the focal species' vocalization as well as realistic examples containing the type of interfering background noise experienced at the site. Recordings of non-focal species and of random audio from the study site were used as negative examples, i.e., potentially similar sounding vocalizations and background noise which the classifier was trained to identify as non-target sounds. The amount of data for each category can be found in Table 1. Using non-bat analysis mode, Kaleidoscope was then employed to scan and cluster the recordings from the training dataset, using 2.0 max distance from cluster center to include inputs, a 5.33ms FFT window, 12 max states, 0.5 max distance from cluster center for building clusters, and 500 max clusters. Among all the resulting clusters which contained at least one detection of the focal species, detections were manually re-classified as either the focal species or noise. Clusters which did not contain the focal species were left as is. These edited cluster IDs were then used to create a new clustering algorithm. The training and re-clustering steps were repeated for multiple iterations until the accuracy reached 80% or improvement plateaued, resulting in the final trained classifiers.

Automatic detection and results cleaning

Trained classifiers for each focal species were used to scan through the entire two-year audio dataset for each site and automatically detect all occurrences of the target vocalizations. As compared with other acoustic clustering software, Kaleidoscope tends to produce false positives (Knight et al. 2017), so all automatic positive detections were manually verified for accuracy and false positives were removed (Table 1). Because all positive detections were verified by a trained human observer, the accuracy of the detections used in the results was estimated at 100%. The presence or absence of each focal species was manually assessed in 1,000 audio files and compared with classifier outputs to estimate the false negative rate and the recall rate (Table 1). False negative rate was the percentage of audio recordings where the focal species was present but not

detected by the classifier. Recall rate is the proportion of all vocalizations that were successfully detected by the classifier (true positives/(true positives + false negatives)).

Hosted file

image2.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

Table 1. Parameters and input data used to train each species classifier. Training parameters: parameters input into Kaleidoscope Pro to determine whether or not a sound could potentially refer to the focal species and should be extracted from the ~70,000 hour acoustic dataset. Training data: audio recordings used to train the species classifiers; each training dataset includes vocalizations from the focal species (focal), vocalizations from other similar sounding species found at the same site (non-focal), audio recorded at the study site, and clear recordings from the sound library Xeno-Canto (www.xeno-canto.org). Verified detections: total number of times the focal species was accurately detected in the ~70,000 hour audio dataset, manually verified to remove false positives. The presence or absence of each focal species was manually assessed in 1,000 audio files and compared with classifier outputs to estimate the false negative rate and the recall rate.

Seasonality Index

A novel seasonality index (S) was developed for this dataset to assess how strongly seasonal the vocal activity was for each species. This index defines seasonal behavior as behavior concentrated during a particular time of year, occurring at the same time across years. The index is made up of two components: signal strength (R) and directional agreement (D) (Formula 1).

Signal strength (R) is a measure of how concentrated vocal activity is within a single time of year. To calculate this, the number of vocally active hours per day is averaged by month and each monthly value is treated as a vector, where the direction of the vector corresponds with the month of the year, placed radially on a circle (Figure 2). The magnitude of the sum of all 12 vectors is divided by the total magnitude of all vectors to get signal strength (R) (Formula 2, Figure 2iii). Subscript i indexes the month. Signal strength (R) has a maximum value of 1 when all activity is concentrated within a single month, and a minimum value of 0 when activity is equally distributed throughout the year.

Directional agreement (D) is a measure of the similarity between years. To calculate directional agreement (D), all 12 monthly vectors are added together for each year to find the direction of the resultant vector ϑ . Directional agreement is the inverse of the difference between $\vartheta_{\text{year 1}}$ and $\vartheta_{\text{year 2}}$ (Formula 3, Figure 2ii). Directional agreement (D) has a maximum value of 1 when peak vocal activity occurs at the same time in both years, and a minimum value of 0 when peak activity happens at opposite times of year between the two years; for example, if peak activity occurred on January 1st of the first year and July 1st of the second, then D=0.

The seasonality index (S) will have a maximum value of 1 when vocal activity is concentrated entirely in the same single month in both years. S will have a minimum value of zero either if activity is evenly distributed throughout the year, or if peak activity happens at opposite times of year in the two years. R code used to calculate the seasonality index is available in the Supporting Information.

Formula 1:

$$S = R * D = \textit{Seasonality index}$$

Formula 2:

Formula 3:

$$\theta_i = \textit{direction of the sum of all vectors } [\vec{v}_1 : \vec{v}_{12}] \textit{ from year}_i$$

$$dd = |\theta_1 - \theta_2| = \text{directional disagreement}$$

$$\text{if } (|\theta_1 - \theta_2| > \pi), \text{ then } dd = (2\pi - |\theta_1 - \theta_2|)$$

Hosted file

image3.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

Figure 2: Panel (i) Visual representation of vectorized monthly activity. All units are radians, not degrees. Months are placed radially on a circle, with January at 0 radians. For each monthly vector \vec{v}_i , the magnitude of the vector is the number of vocally active hours per month, and the direction of the vector is dictated by the month's identity. These monthly vectors are used to calculate R . Panel (ii) Visual representation of the directional agreement between years. Panel (iii) Visual representation of the magnitude of the sum of all vectors versus the total magnitude of all vectors.

Focal species: historically native versus parkland colonizers

The number of focal species was limited to nine due to logistical constraints; training a species classifier takes a degree of time and effort. These nine species were selected because theirs were the vocalizations which appeared most frequently in the audio dataset. The focal bird species from Singapore were divided *post-hoc* into two main categories: recent parkland colonizers and historically native forest species. Parkland colonizers are not what would typically be considered invasive species; these parkland species are native to the broader Sundaic region, but did not historically occur within Singapore because they are not adapted to closed canopy forest. Much of the Sundaic bioregion is climatically everwet and has historically been dominated by rainforest. However, deciduous woodland or coastal scrub, with their distinct avifauna, exist in scattered pockets throughout the area, or have been the predominant habitat type in some peripheral regions of the Sundaic region, such as eastern Java and northern peninsular Malaysia. Parks and gardens in urbanized Singapore more closely resemble woodland than rainforest and have been colonized by such woodland species over the past few decades. While all the recording stations in this study were inside forest, not parkland, focal species recorded included both historically native species and more recent colonizers. The focal species in this study include four recent colonizers, all of which have had breeding populations in Singapore for less than 100 years, and five forest species historically native to Singapore. The recent colonizers in Singapore are Black-naped Oriole (*Oriolus chinensis*, established ~1925), Lineated Barbet (*Psilopogon lineatus*, established ~1997), Straw-headed Bulbul (*Pycnonotus zeylanicus*, established on the main island ~1980), and Asian Koel (*Eudynamis scolopaceus*, established ~1950) (Gibson-Hill 1950, Wells 2010, Lim 2019). The historically native forest species in Singapore are Little Spiderhunter (*Arachnothera longirostra*), Drongo Cuckoo (*Surniculus lugubris*), Rufous-tailed Tailorbird (*Orthotomus sericeus*), Pin-striped Tit-babbler (*Mixornis gularis*), and Short-tailed Babbler (*Pellorneum malaccense*).

RESULTS

Historically native species were more vocally seasonal than recent parkland colonizers. The seasonality indices of native forest species ranged from 0.25–0.69. The seasonality indices of parkland colonizers were lower, ranging from 0.01–0.25 (Figure 3, Figure 4). Only the most seasonal species, Little Spiderhunters and Drongo-cuckoos, were entirely silent for months at a time. Species with slightly weaker seasonal trends in vocal behavior, including Rufous-tailed Tailorbirds and Pin-striped Tit-babblers, had a distinct season of heightened vocal activity but could still be heard to a lesser extent during the off season. In contrast, parkland colonizers like Straw-headed Bulbuls and Asian Koels did not follow any seasonal pattern – peak vocal activity occurred in different months between the two years and concentrated irregularly throughout the year.

The peak vocal season for most species was around June. Of the five focal native forest species, all but one had their peak seasons in May-June. Little Spiderhunters, the only nectarivore, had a peak vocal season earlier in the year, in March (Figure 3, Figure 5, Table 2). Lineated Barbets did not show a seasonal trend but did have an interannual trend – they were heard more often in year two than in year one of the study.

Hosted file

image4.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

(A)

Hosted file

image5.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

(B)

(C)

Hosted file

image6.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

Hosted file

image7.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

(D)

(E)

Hosted file

image8.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

Hosted file

image9.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

(F)

(G)

Hosted file

image10.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

Hosted file

image11.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

(H)

Hosted file

image12.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

(I)

Figure 3. Vocal activity of focal species in Singapore throughout the seasons: (a) Little Spiderhunter, (b) Drongo-cuckoo, (c) Rufous-tailed Tailorbird, (d) Pin-striped Tit-babbler, (e) Short-tailed Babbler, (f) Black-naped Oriole, (g) Lineated Barbet, (h) Straw-headed Bulbul, and (i) Asian Koel. Sub-panels: (i) spectrogram of the focal species' main vocalization, i.e., the specific motif detected by the species classifier; (ii) radar plot, lines indicate number of vocally active hours per month, direction and magnitude of arrows indicate the directionality and signal strength R of year 1 (red) and year 2 (black) respectively. Year 1 extends from June 2020-May 2021. Year 2 extends from June 2021-May 2022; (iii) hourly vocalizations detected with Kaleidoscope Pro using single species classifier, manually verified to remove false positives. White space indicates missing data. Each pixel represents one hour, the color of the pixel is the number of times the focal species' vocalization was accurately detected during that hour on a logarithmic scale. Species illustrations from Eaton et al. (2021) with permission.

Hosted file

image13.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

Figure 4. Species' seasonality indices by native versus colonizer status. The seasonality index reaches a maximum of 1 when all vocal activity occurs within a single month of the year and peak activity occurs at the same time in both years. The seasonality index reaches a minimum of 0 when vocal activity is equally distributed through all 12 months, or if peak vocal activity occurs at opposite times during the two years.

Hosted file

image14.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

Ταβλε 2. Σεασοναλιτψ ινδιδες βψ σπεσιες. P ις α μεασυρε οφ σηναλ στρενγη, ορ ηωω ζονςεντρατεδ οσαλ αστυιτψ ις ωιτην α σπεσιφισ τιμε οφ ψεαρ. $P=1$ ωην αλλ οσαλ αστυιτψ ις ζονςεντρατεδ ιντο α σινγλε μοντη, ανδ $P=0$ ωην οσαλ αστυιτψ ις εχουαλλψ διστριβυτεδ τηρουγηουτ της ψεαρ. θ ις της τιμε οφ ψεαρ ωην οσαλ αστυιτψ ωας ατ ιτς πεακ, μεασυρεδ ιν ραδιανς· μοντη ναμες αρε ινςλυδεδ ιν παρεντησεις φορ ζονενιενσε. $P_{Oεραλλ}$ ις P οφ της φυλλ 2-ψεαρ τιμε σεριες, ανδ $\theta_{Oεραλλ}$ ις θ οφ της φυλλ 2-ψεαρ τιμε σεριες.

Hosted file

image15.emf available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

Φιγυρε 5. οσαλ σεασοναλ διρεστιαλιτψ οφ αλλ ινε σπεσιες. ζστορ μαγνιτυδε ις Σεασοναλιτψ Ινδεξ (Σ). ζστορ διρεστιαλιτψ ις $\theta_{Oεραλλ}$, της μεαν διρεστιαλιτψ οφ της φυλλ τωο-ψεαρ τιμε σεριες. Γρεεν: Ηιστορισαλλψ νατιε

φορεστ σπερσιες: Ορανγε: Ρερεντ παρκλανδ ζολονιζερ.

Hosted file

image16.emf available at <https://aurea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

Figure 6. Seasonality index versus approximate date when breeding population was established, shown across the four parkland colonizer species in Singapore.

DISCUSSION

Urbanization and phenology

Phenology is an aspect of a species' ecological niche which is dynamically associated with both habitat and climate, and vocal seasonality is typical of most birds globally, even in equatorial regions where the climate is nearly aseasonal (Thomson 1950, Hau et al. 1998, Beebe et al. 2005, Berman et al. 2023). Among the panel of nine focal species in this study, some sang seasonally as expected, while others did not. Historically native species adapted to forest interiors sang seasonally, while species which have only established breeding populations within the last few decades, and which are adapted to more open habitats, sang aseasonally. Singapore has undergone dramatic urbanization over the last 200 years. That urbanization has led to changes in land cover, including the introduction of open parkland habitat resembling woodlands, which in turn has led to a shift in species composition and the colonization of woodland-adapted birds. Our results suggest that this conversion of forest into parkland and urban areas has not only altered the species composition of Singapore, but in doing so may have also led to an altered community phenology. While it is clear from the data that historically native forest species are more seasonal in their song than the more recently established species, it is less obvious why these two groups of species should have distinct phenologies. Some potential explanations include dietary differences, or an initial transitional period of aseasonality for newly established populations that may last for decades. In the following paragraphs we discuss the potential factors driving these phenological differences.

Seasonal availability of preferred foods may differ between species

One potential explanation for why colonizer species are less seasonal than native forest species may be differences in food availability. Translocation of birds to sites with high year-round food availability can lead to a prolonged or year-round breeding season (Komdeur 1996). While all audio recorders, and therefore all detected birds, were in forested sites, colonizer species are generally more abundant nearer the forest edge, in more open habitat patches and in parkland. Man-made parks have a different floral species composition as compared to natural forests, and it is possible that food availability does not correlate as closely with seasonal cycles in manicured parklands. Many genera of bird-dispersed fruit-bearing plants which are common in Singaporean forests, including *Litsea*, *Myristica*, *Santiria*, and *Timonius*, follow a masting pattern of reproduction (Corlett 1990). Mast fruiting most often occurs in June – August (Corlett 1990, Chong et al. 2016, Corlett 2019), coinciding with the fledging period of the native breeding season (Berman et al. 2023). In contrast, fruiting figs, another staple of the frugivorous diet, fruit continuously on the population level and provide a stable year-round food supply (Cannon et al. 2007; Corlett 2019). Figs are common in forest, but are especially abundant in parklands. It is possible that a lack of masting species in parklands may reduce the benefits of seasonal breeding among parkland-adapted birds. Two of the four parkland colonizers among our target species are primarily frugivorous (Straw-headed Bulbul, Lineated Barbet), and the other two are known to take fruit at least seasonally or occasionally (Asian Koel, Black-naped Oriole), supporting the potential importance of fruit availability for the phenology of these species.

Aseasonality may be adaptive in newly established populations

Recent parkland colonizers may be less seasonal because they have not yet adapted their phenology to the local cycle. Breeding seasonally is adaptively advantageous (Ims 1990), but introduced species in tropical

habitats sometimes do breed aseasonally (Rodda and Savidge 2007, Beard et al. 2009, Brodie et al. 2021). Introduced populations which initially bred year-round have been known to become seasonal breeders after several generations in a new habitat (Hengeveld 1994).

Year-round breeding may be adaptive for newly established species expanding into an unoccupied niche (Hengeveld 1994), but for populations at carrying capacity, the inability to synchronize breeding with the time of peak food availability may lead to lower survivorship of young and excessive metabolic stress on parents (Thomas 2001). A lack of synchronized breeding may also reduce the chance of finding a suitable partner that is at the same reproductive and hormonal stage in the seasonal cycle. For newly established populations, it may take time to attune the biological clock to a new set of environmental signals, especially if those signals are weak (Baker and Ranson 1938). If this hypothesis is true, we might expect the most recent colonizers to be the least seasonal, and for populations to become more seasonal over time. The data from our limited panel of species only partially supports this pattern (Figure 6). Among the four parkland colonizers in our panel, Black-naped Orioles have been present in Singapore the longest, first establishing a breeding population in 1925 due to the conversion of forests into plantations (Wells 2010). At the same time, Black-naped Orioles exhibit the strongest seasonality among our four parkland colonizers (Figure 4, Figure 6), suggesting that their extended residency may have provided them with sufficient time to converge on a new seasonal rhythm. However, there is no clear linear pattern between seasonality and establishment dates among the other three species (Figure 6), suggesting that a larger species panel may be needed to confirm this relationship.

Conclusions

Recent parkland colonizers were less seasonal than historically native forest species in their vocal phenologies, suggesting that either a) man-made parklands may promote aseasonal phenologies among parkland-adapted birds, or b) newly arrived species may undergo an initial period of transitional aseasonality. In either case, the conversion of forest into parkland and urban areas which has occurred in Singapore over the last 200 years has altered not only the community of species present, but also the phenology of that community. This altered phenology is yet another way that human habitat modification may disrupt tropical communities. While continuous or aseasonal breeding may be advantageous to species expanding their ranges, it is expected to lead to reduced reproductive success for species already in decline.

REFERENCES

- Abernethy, K., Bush, E. R., Forget, P. M., Mendoza, I., & Morellato, L. P. C. (2018). Current issues in tropical phenology: a synthesis. *Biotropica*, 50(3), 477-482. <https://doi.org/10.1111/btp.12558>
- Baker, J. R. (1939). The relation between latitude and breeding seasons in birds. In *Proceedings of the Zoological Society of London* (Vol. 108, No. 4, pp. 557-582). Oxford, UK: Blackwell Publishing Ltd. <https://doi.org/10.1111/j.1096-3642.1939.tb00042.x>
- Baker, J. R., & Ranson, R. M. (1938). The breeding seasons of southern hemisphere birds in the northern hemisphere. In *Proceedings of the Zoological Society of London* (Vol. 108, No. 1, pp. 101-141). Oxford, UK: Blackwell Publishing Ltd. <https://doi.org/10.1111/j.1469-7998.1938.tb00024.x>
- Bardeli, R., Wolff, D., Kurth, F., Koch, M., Tauchert, K. H., & Frommolt, K. H. (2010). Detecting bird sounds in a complex acoustic environment and application to bioacoustic monitoring. *Pattern Recognition Letters*, 31(12), 1524-1534. <https://doi.org/10.1016/j.patrec.2009.09.014>
- Beard, K. H., Price, E. A., & Pitt, W. C. (2009). Biology and Impacts of Pacific Island Invasive Species. 5. *Eleutherodactylus coqui*, the Coqui Frog (*Anura: Leptodactylidae*) 1. *Pacific Science*, 63(3), 297-316. <https://doi.org/10.2984/049.063.0301>
- Beebe, K., G. E. Bentley, and Michaela Hau. (2005) A seasonally breeding tropical bird lacks absolute photorefractoriness in the wild, despite high photoperiodic sensitivity. *Functional Ecology* 19.3, 505-512. <https://doi.org/10.1111/j.1365-2435.2005.00994.x>
- Bell, H.L., (1982). A bird community of lowland rain forest in New Guinea. 2 Seasonality. *Emu*, 82(2), 65-74. <https://doi.org/10.1071/MU9820065>
- Berman, L., Li, D., Shufen, Y., Kennewell, M., & Rheindt, F. (2023). Bird breeding season linked to sunshine hours in a marginally seasonal equatorial climate. *Journal of Ornithology*, 164(1), 125-138. <https://doi.org/10.1007/s10336-022-02009-9>
- Borker, A. L., Halbert, P., Mckown, M. W., Tershy, B. R., & Croll, D. A. (2015). A comparison of automated and traditional monitoring

techniques for marbled murrelets using passive acoustic sensors. *Wildlife Society Bulletin*, 39(4), 813-818. <https://doi.org/10.1002/wsb.608> Bota, G., Manzano-Rubio, R., Catalán, L., Gómez-Catasús, J., & Pérez-Granados, C. (2023). Hearing to the unseen: AudioMoth and BirdNET as a cheap and easy method for monitoring cryptic bird species. *Sensors*, 23(16), 7176. <https://doi.org/10.3390/s23167176> Brodie, S., Yasumiba, K., Towsey, M., Roe, P., & Schwarzkopf, L. (2021). Acoustic monitoring reveals year-round calling by invasive toads in tropical Australia. *Bioacoustics*, 30(2), 125-141. <https://doi.org/10.1080/09524622.2019.1705183> Brumm, H., & Zollinger, S. A. (2013). Avian vocal production in noise. In *Animal communication and noise* (pp. 187-227). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-41494-7_7 Cannon, C. H., Curran, L. M., Marshall, A. J., & Leighton, M. (2007). Beyond mast-fruited events: Community asynchrony and individual dormancy dominate woody plant reproductive behavior across seven Bornean forest types. *Current Science*, 1558-1566. <https://www.jstor.org/stable/24099085> Chisholm, R. A., Giam, X., Sardanandan, K. R., Fung, T., & Rheindt, F. E. (2016). A robust nonparametric method for quantifying undetected extinctions. *Conservation Biology*, 30(3), 610-617. <https://doi.org/10.1111/cobi.12640> Chisholm, R. A., Kristensen, N. P., Rheindt, F. E., Chong, K. Y., Ascher, J. S., Lim, K. K., ... & Sin, Y. K. (2023). Two centuries of biodiversity discovery and loss in Singapore. *Proceedings of the National Academy of Sciences*, 120(51), e2309034120. <https://doi.org/10.1073/pnas.2309034120> Chong, K. Y., Chong, R., Tan, L. W., Yee, A. T., Chua, M. A., Wong, K. M., & Tan, H. T. (2016). Seed production and survival of four dipterocarp species in degraded forests in Singapore. *Plant Ecology & Diversity*, 9(5-6), 483-490. <https://doi.org/10.1080/17550874.2016.1266404> Corlett, R., (1919). *The ecology of tropical East Asia*. Oxford University Press, USA. Corlett, R., (1990) Flora and reproductive phenology of the rain forest at Bukit Timah, Singapore. *Journal of Tropical Ecology*, pp.55-63. <https://doi.org/10.1017/S0266467400004028> Deichmann, J. L., Acevedo-Charry, O., Barclay, L., Burivalova, Z., Campos-Cerqueira, M., d'Horta, F., ... & Mitchell Aide, T. (2018). It's time to listen: there is much to be learned from the sounds of tropical ecosystems. *Biotropica*, 50(5), 713-718. <https://doi.org/10.1111/btp.12593> Eaton, J. A., van Balen, B., Brickley, N. W., & Rheindt, F. E. (2021). *Birds of the Indonesian Archipelago. Greater Sundas and Wallacea* (second edition). Lynx Edicions. Barcelona. Frommolt, K. H., Tauchert, K. H., & Koch, M. (2008). Advantages and disadvantages of acoustic monitoring of birds—realistic scenarios for automated bioacoustic monitoring in a densely populated region. In *Proceedings of the international expert meeting on IT-based detection of bioacoustical patterns* (Vol. 235, pp. 83-92). Gibson-Hill, C.A., 1950. A Checklist of the birds of Singapore Island. *Bulletin of Raffles Museum*, 21:132-183 Hau, M., Wikelski, M., & Wingfield, J. C. (1998). A neotropical forest bird can measure the slight changes in tropical photoperiod. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265(1391), 89-95. <https://doi.org/10.1098/rspb.1998.0268> Hengeveld, R. (1994). Small-step invasion research. *Trends in Ecology & Evolution*, 9(9), 339-342. Hill, A. P., Prince, P., Pina Covarrubias, E., Doncaster, C. P., Snaddon, J. L., & Rogers, A. (2018). AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods in Ecology and Evolution*, 9(5), 1199-1211. <https://doi.org/10.1111/2041-210X.12955> Ims, R. A. (1990). The ecology and evolution of reproductive synchrony. *Trends in ecology & evolution*, 5(5), 135-140. Jahn, O., Ganchev, T. D., Marques, M. I., & Schuchmann, K. L. (2017). Automated sound recognition provides insights into the behavioral ecology of a tropical bird. *PloS one*, 12(1), e0169041. <https://doi.org/10.1371/journal.pone.0169041> Knight, E., Hannah, K., Foley, G., Scott, C., Brigham, R., & Bayne, E. (2017). Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. *Avian Conservation and Ecology*, 12(2). <https://doi.org/10.5751/ACE-01114-120214> Komdeur, J. (1996). Seasonal timing of reproduction in a tropical bird, the Seychelles warbler: a field experiment using translocation. *Journal of Biological Rhythms*, 11(4), 333-346. <https://doi.org/10.1177/074873049601100407> Lim, K. S. (2019). Birds of Bukit Timah Nature Reserve, Singapore. *Gard. Bull. Singapore*, 71(Suppl 1), 185-208. Manzano-Rubio, R., Bota, G., Brotons, L., Soto-Largo, E., & Perez-Granados, C. (2022). Low-cost open-source recorders and ready-to-use machine learning approaches provide effective monitoring of threatened species. *Ecological Informatics*, 72, 101910. <https://doi.org/10.1016/j.ecoinf.2022.101910> Moore, I. T., Bonier, F., & Wingfield, J. C. (2005). Reproductive asynchrony and population divergence between two tropical bird populations. *Behavioral Ecology*, 16(4), 755-762. <https://doi.org/10.1093/beheco/ari049> Oliver, R. Y., Ellis, D. P., Chmura, H. E., Krause, J. S., Perez, J. H., Sweet, S. K., ... & Boelman,

N. T. (2018). Eavesdropping on the Arctic: Automated bioacoustics reveal dynamics in songbird breeding phenology. *Science Advances*, 4(6), eaaq1084. <https://doi.org/10.1126/sciadv.aaq1084>

Perez-Granados, C., & Schuchmann, K. L. (2020). Illuminating the nightlife of two Neotropical nightjars: vocal behavior over a year and monitoring recommendations. *Ethology Ecology & Evolution*, 32(5), pp. 466-480. <https://doi.org/10.1080/03949370.2020.1753117>

Perkins, A. J., Maggs, H. E., Wilson, J. D., & Watson, A. (2013). Delayed mowing increases corn bunting *Emberiza calandra* nest success in an agri-environment scheme trial. *Agriculture, ecosystems & environment*, 181, 80-89. <https://doi.org/10.1016/j.agee.2013.09.010>

Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H. and Pieretti, N., (2011). Soundscape ecology: the science of sound in the landscape. *BioScience*, 61(3), pp.203-216. <https://doi.org/10.1525/bio.2011.61.3.6>

Pollock, H. S., Brawn, J. D., & Cheviron, Z. A. (2021). Heat tolerances of temperate and tropical birds and their implications for susceptibility to climate warming. *Functional Ecology*, 35(1), 93-104. <https://doi.org/10.1111/1365-2435.13693>

R Core Team (2024). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

Ralph, C. J., & Fancy, S. G. (1994). Timing of breeding and molting in six species of Hawaiian honeycreepers. *Condor*, 96(1), 151-161. <https://doi.org/10.2307/1369072>

Rodda, G. H., & Savidge, J. A. (2007). Biology and impacts of Pacific island invasive species. 2. *Boiga irregularis*, the brown tree snake (Reptilia: Colubridae) 1. *Pacific Science*, 61(3), 307-324. [https://doi.org/10.2984/1534-6188\(2007\)61\[307:BAIOPI\]2.0.CO;2](https://doi.org/10.2984/1534-6188(2007)61[307:BAIOPI]2.0.CO;2)

Sadanandan, K.R., Tan, H. Z., Lim, H. Y., Tan, Y. G., Lee, G., Chan, L., Pei, Y., Rheindt, F.E., and Baldwin, M. W. (2023). Spatial and temporal resource partitioning in a mixed species colony of echolocating birds. *Ecology and Evolution*, 13(2), e9805. <https://doi.org/10.1002/ece3.9805>

Scheffers, B. R., De Meester, L., Bridge, T. C., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., ... & Watson, J. E. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, 354(6313), aaf7671. <https://doi.org/10.1126/science.aaf7671>

Schwartz, M. D. (Ed.). (2013). *Phenology: an integrative environmental science* (2nd ed.). Springer.

Serle, W. (1981). The breeding season of birds in the lowland rainforest and in the montane forest of West Cameroon. *Ibis*, 123(1), 62-74. <https://doi.org/10.1111/j.1474-919X.1981.tb00173.x>

Shonfield, J., & Bayne, E. (2017). Autonomous recording units in avian ecological research: current use and future applications. *Avian Conservation and Ecology*, 12(1).

Snow, D. W., & Snow, B. K. (1964). Breeding seasons and annual cycles of Trinidad landbirds. *Zoologica*, 49(1), 1-39.

Sodhi, N. S. (2002). The effects of food-supply on Southeast Asian forest birds. *Ornithological Science*, 1(1), 89-93. <https://doi.org/10.2326/osj.1.89>

Steward, J. S., Round, P. D., & Milne, J. R. (2013). Food availability fails to explain asynchronous breeding of two syntopic Oriental trogons. *Condor*, 115(4), 838-846. <https://doi.org/10.1525/cond.2013.120005>

Stouffer, P. C., Johnson, E. I., & Bierregaard Jr, R. O. (2013). Breeding seasonality in central Amazonian rainforest birds. *Auk*, 130(3), 529-540. <https://doi.org/10.1525/auk.2013.12179>

Stowell, D., Wood, M. D., Pamula, H., Stylianou, Y., & Glotin, H. (2019). Automatic acoustic detection of birds through deep learning: the first bird audio detection challenge. *Methods in Ecology and Evolution*, 10(3), 368-380. <https://doi.org/10.1111/2041-210X.13103>

Stutchbury, B. J., & Morton, E. S. (2001). *Behavioral ecology of tropical birds*. Academic Press.

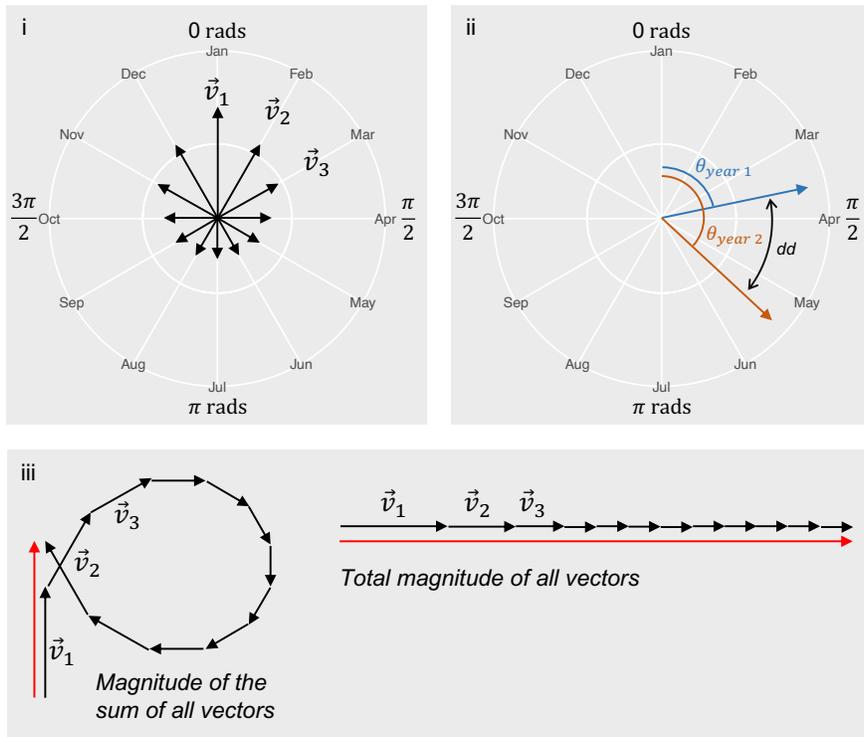
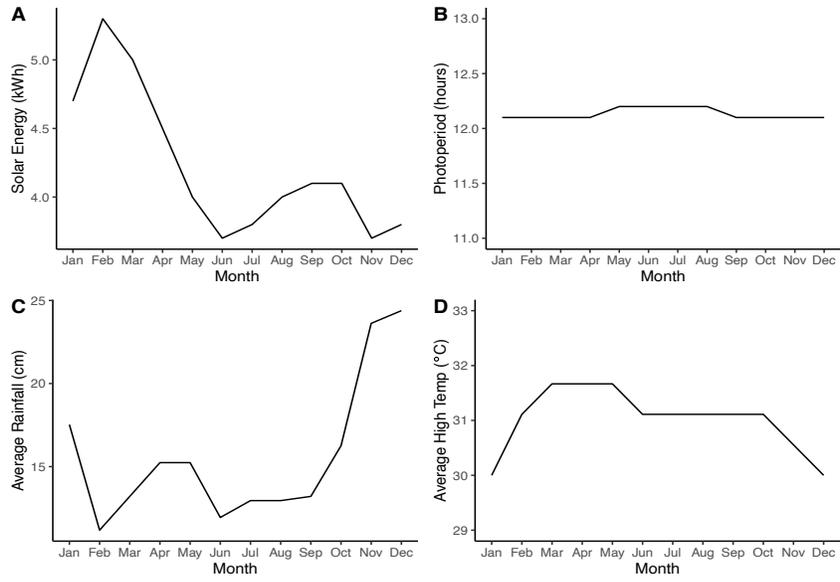
Thomas, D. W., Blondel, J., Perret, P., Lambrechts, M. M., & Speakman, J. R. (2001). Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science*, 291(5513), 2598-2600. <https://doi.org/10.1126/science.1057487>

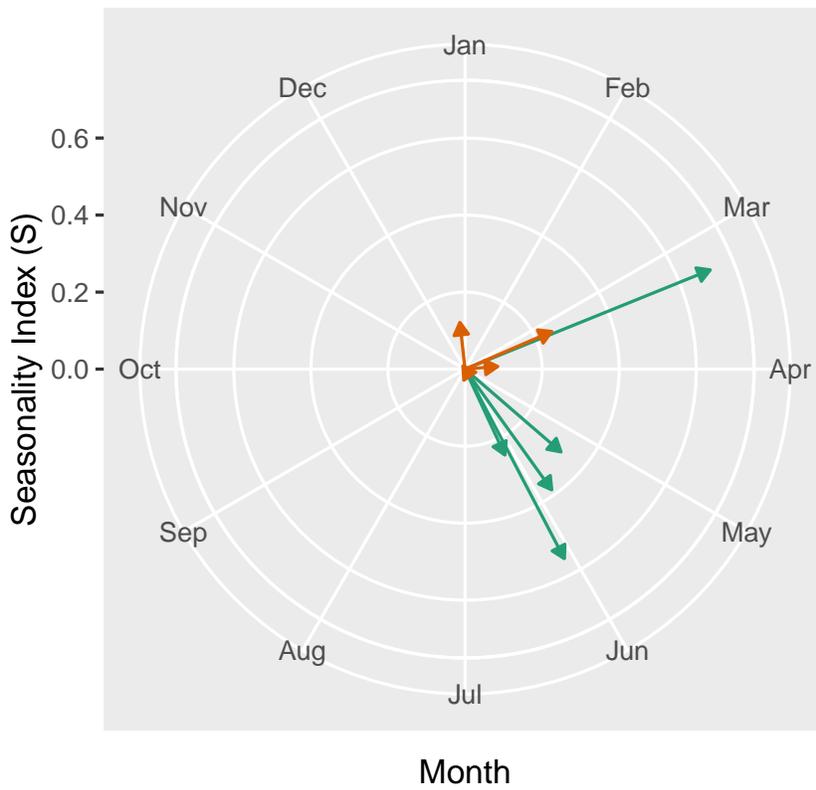
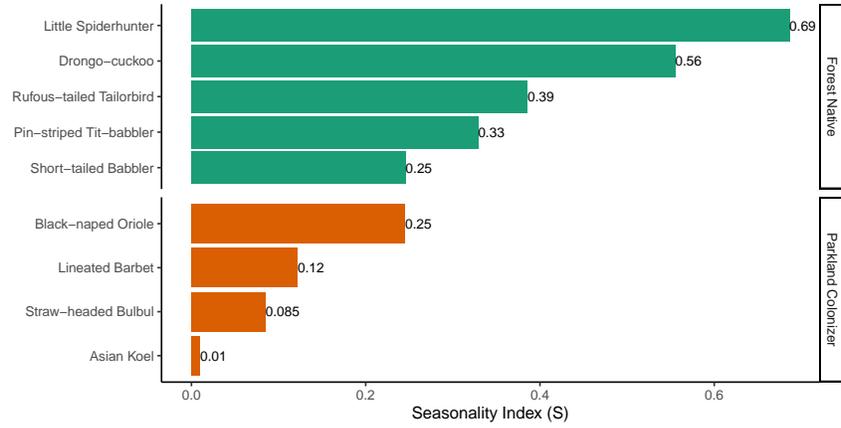
Thomson, A. L. (1950). Factors determining the breeding seasons of birds: an introductory review. *Ibis*, 92(2), 173-184. <https://doi.org/10.1111/j.1474-919X.1950.tb01748.x>

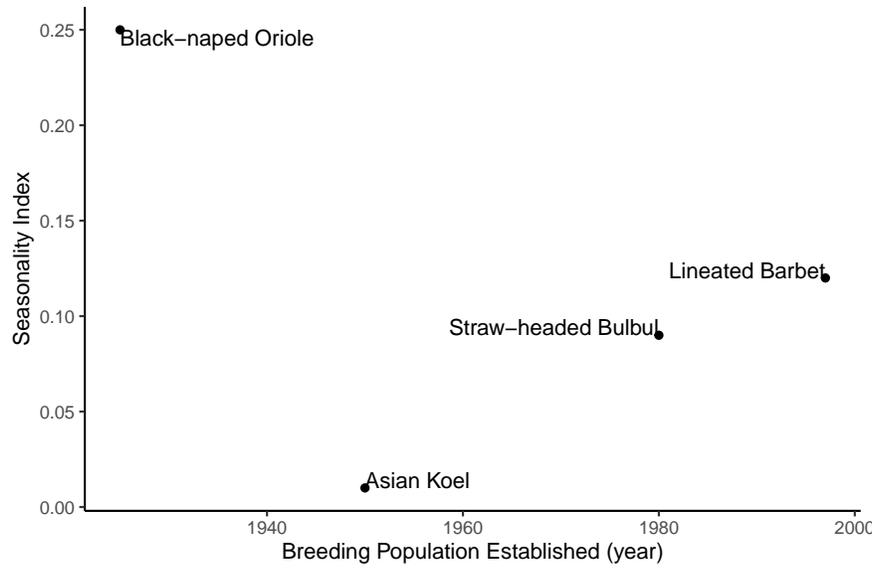
Wells, D. R. (2010). *The Birds of the Thai-Malay Peninsula* (Vol. 2). Bloomsbury Publishing.

Wrege, P. H., & Emlen, S. T. (1991). Breeding seasonality and reproductive success of White-fronted Bee-eaters in Kenya. *Auk*, 108(3), 673-687. <https://doi.org/10.2307/4088107>

Yee, A. T. K., Corlett, R. T., Liew, S. C., & Tan, H. T. (2011). The vegetation of Singapore—an updated map. *Gardens' Bulletin Singapore*, 63(1&2), 205-212.







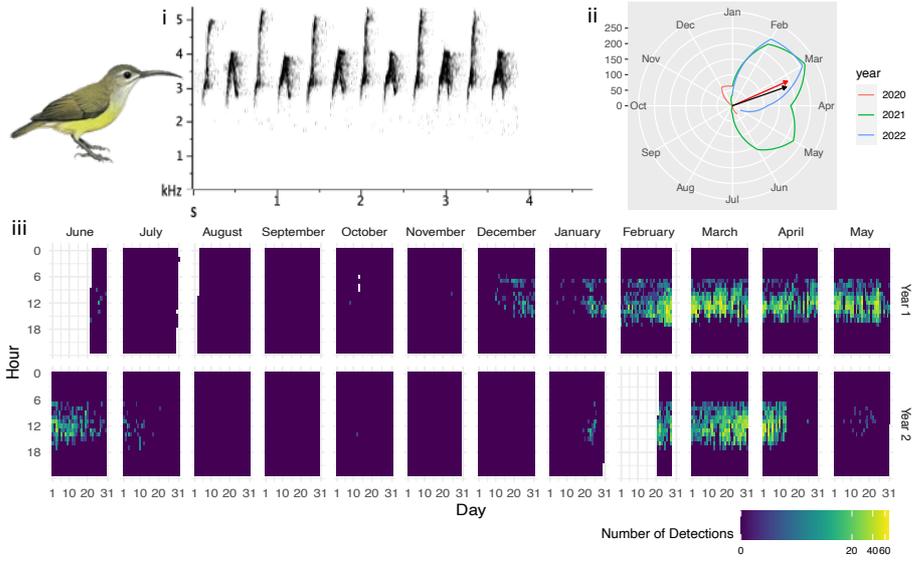
Hosted file

Table 1.xlsx available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

Hosted file

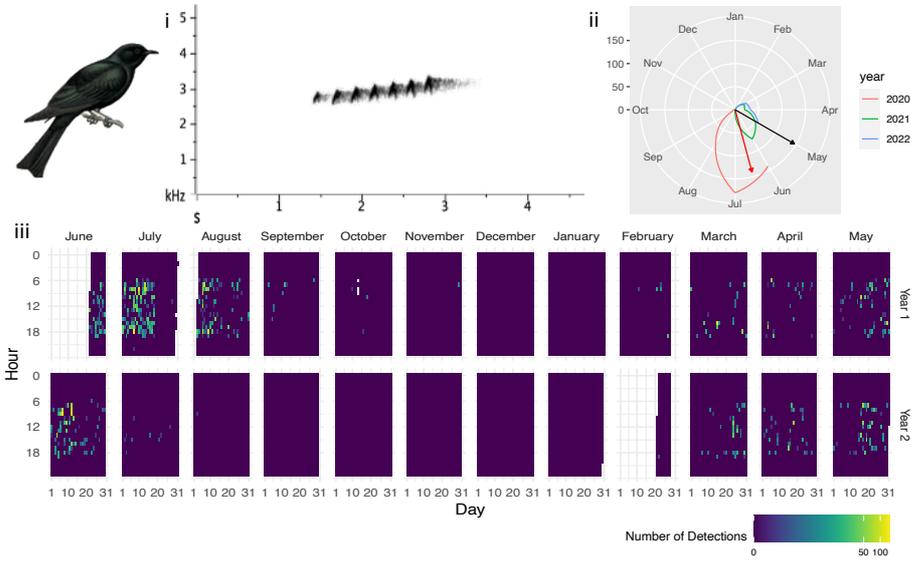
Table 2.xlsx available at <https://authorea.com/users/761505/articles/737555-acoustic-phenology-among-tropical-resident-birds-differs-between-native-forest-species-and-parkland-colonizer-species>

Little Spiderhunter (*A. longirostra*)



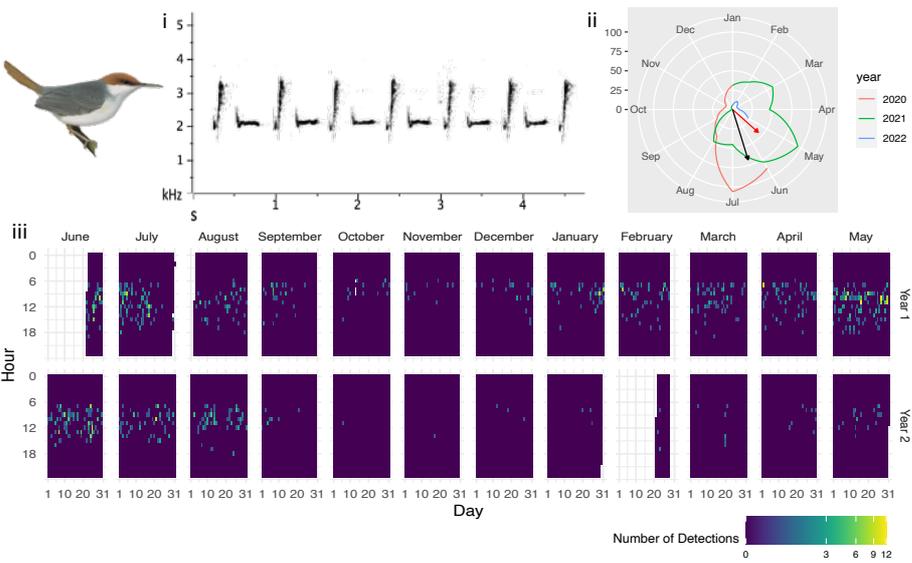
(A)

Drongo-cuckoo (*S. lugubris*)



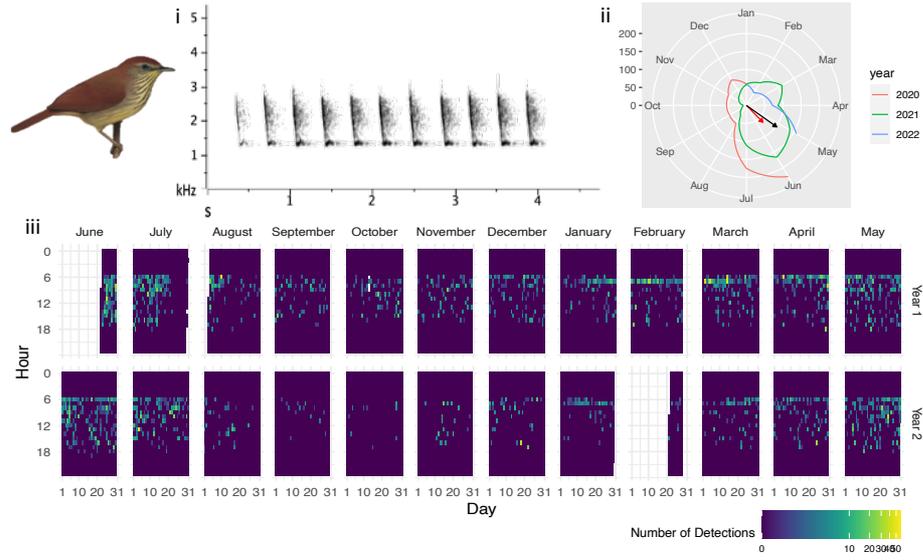
(B)

Rufous-tailed Tailorbird (*O. sericeus*)



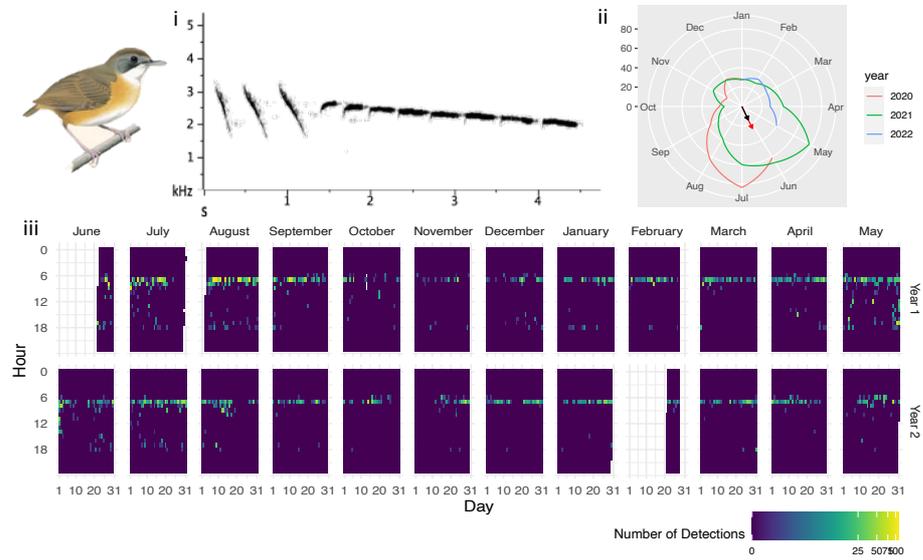
(C)

Pin-striped Tit-babbler (*M. gularis*)



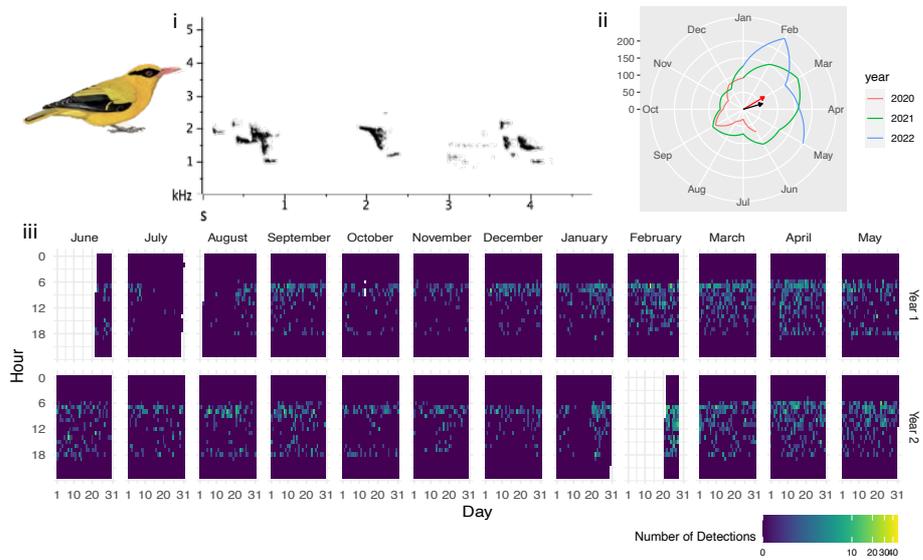
(D)

Short-tailed Babbler (*P. malaccense*)



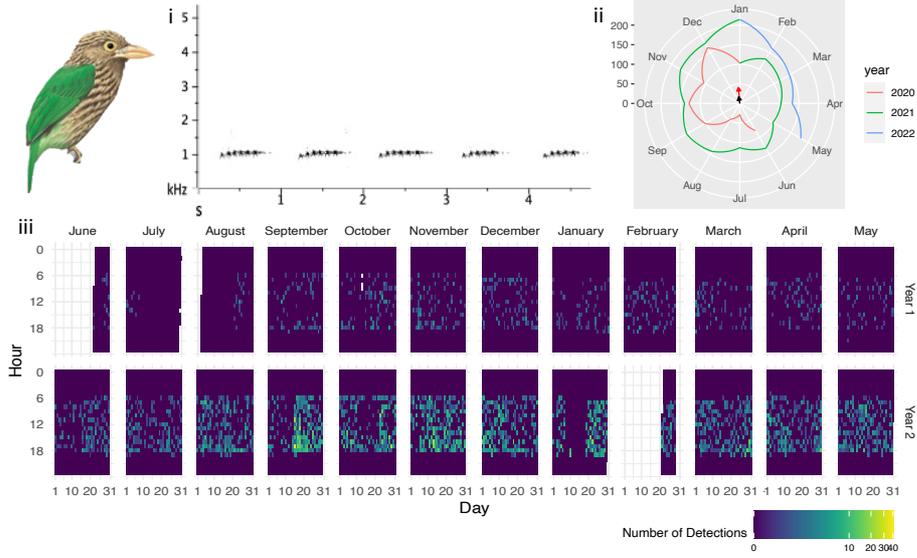
(E)

Black-naped Oriole (*O. chinensis*)



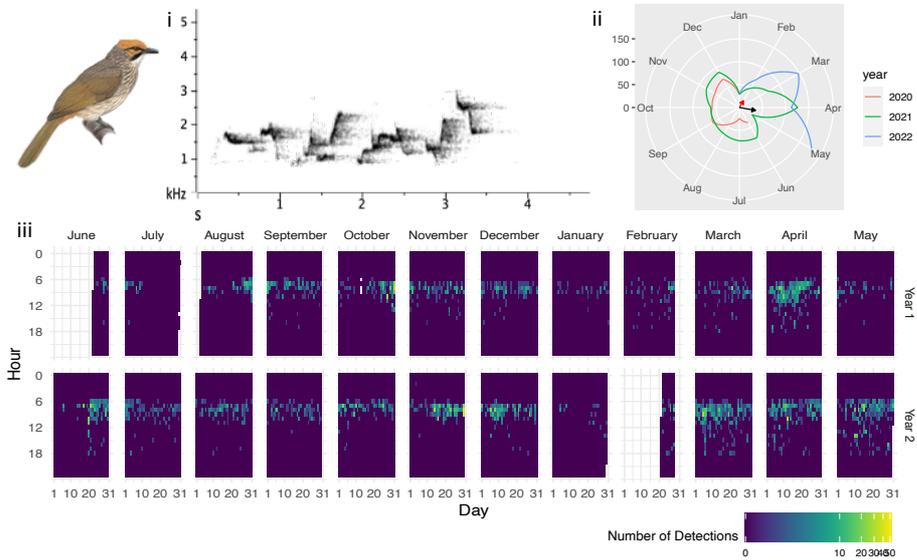
(F)

Lineated Barbet (*P. lineatus*)



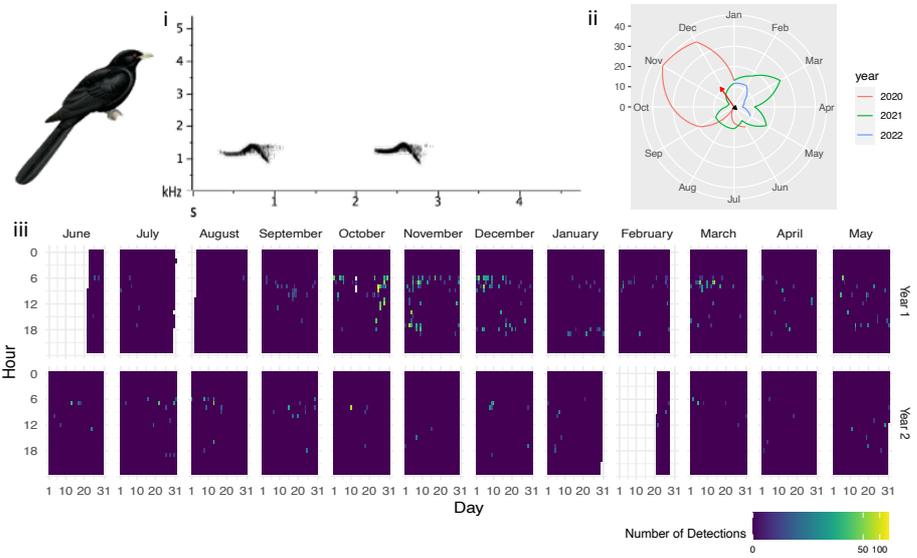
(G)

Straw-headed Bulbul (*P. zeylanicus*)



(H)

Asian Koel (*E. scolopaceus*)



(I)