A forked relationship: Understanding the acoustic communication strategies in sympatric drongos

Dissertation Submitted to
Saurashtra University, Rajkot
in partial fulfillment of Master's Degree in Wildlife Science

By

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Under the Supervision of

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Wildlife Institute of India

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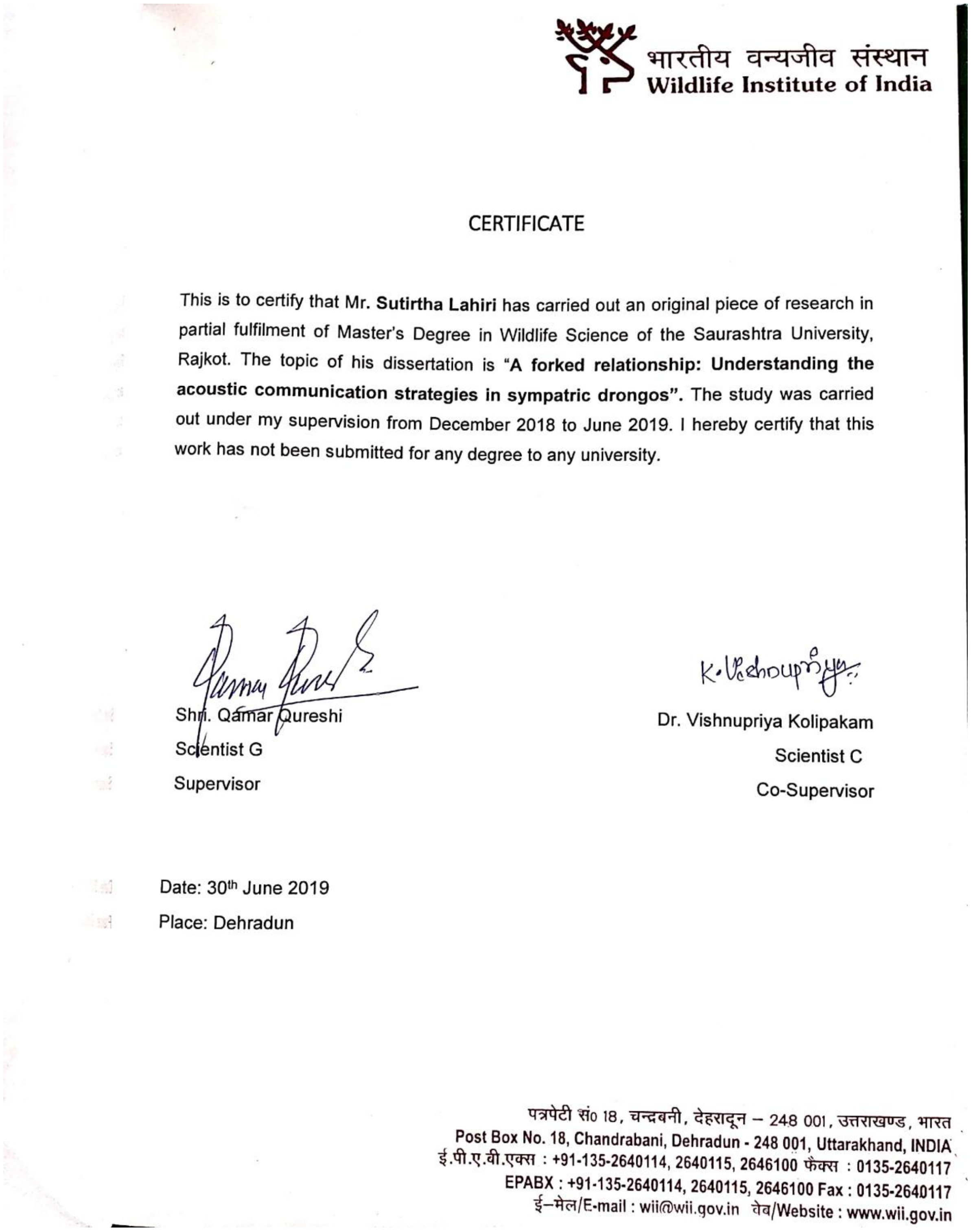
DECLARATION

I, **Sutirtha Lahiri**, hereby declare that the research work entitled **"A forked relationship: Understanding the acoustic communication strategies in sympatric drongos", carried out** in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot is an original piece of research work. This research work was carried out under the supervision of **Shri. Qamar Qureshi and Dr. Vishnupriya Kolipakam**, at the Wildlife Institute of India from December 2018 to June 2019. I hereby declare that this work has not been submitted for any other degree of any university.

Date: June 30th, 2019	Mr. Sutirtha Lahiri
Place: Dehra Dun	(XVI M.Sc. Course)



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Wildlife Institute of India

CERTIFICATE

This is to certify that Mr. **Sutirtha Lahiri** has carried out an original piece of research in partial fulfilment of Master's Degree in Wildlife Science of the Saurashtra University, Rajkot. The topic of his dissertation is **"A forked relationship: Understanding the acoustic communication strategies in sympatric drongos"**. The study was carried out under my supervision from December 2018 to June 2019. I hereby certify that this work has not been submitted for any degree to any university.

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Acknowledgement

Somehow, the task of writing and finishing this section, at a moment when I am about to leave Dehradun by the end of the day, and with the added lure of sitting in the balcony of room 12 of the new hostel, where we spent our very first days here, seems highly daunting. The rains finally brought down the temperature and toned up the green, and the trail and the lake looks beautiful from here! Add to it are the cacophony of the Indian Hawk Cuckoo, the serenading magpie robin, a distant call of the koel and a prinia calling in great alarm, and I am already contemplating a quick walk in the trail. But no, more than just the need to fill this section as yet another part of the thesis, I actually want to give a good amount of time into this section. So, here goes…

If I ever have to begin any acknowledgement, I think it would be a great disservice if I do not mention that without my parents, I would be nothing. Here's to them, for everything that I am. From understanding what my passions are, to telling off all the other family members who couldn't comprehend someone in their family going the 'wild' way and seemingly eating snakes and frogs to sustain, to excitedly reading and sharing everything I write, and to everything else which I will not have the space to add.

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2 EXECUTIVE SUMMARY

The competitive exclusion principle states that ecologically similar species cannot co-exist and will either go extinct or develop diverging traits, the concept of environment filtering regards the environment. Patterns of trait divergence vary depending on whether the species occur in sympatry or in allopatry. Sympatry is defined as the co-occurrence of more than one species in the same geographical area with overlapping ranges. If closely related species occur in sympatry, competition is likely to shape divergence in their ecological as well as in the sensory domain, example acoustic signals.

Diverse animal taxa employ acoustic signals for a variety of functions including mate choice, species identification, resource defence and other ecological and social functions. The primary aim of an acoustic signal is to efficiently communicate information over relatively long distances. This information, however, is subjected to changes and distortions imposed by the physical structure of the habitat, as well as masking interference from co-occurring signals of other acoustically communicating species. Masking interference by background noise or the simultaneously vocalization of other species- especially ones closely related- incur several disadvantages to the vocalizing individual. Signals with similar features have a high potential of interference for the species vocalizing, as well as for the receiver interpreting it. These disadvantages- or costs- could be the failure to respond to appropriate signals and the unnecessary response to territorial or mating signals not meant for them.

However, a number of animals communicate successfully even in noisy and crowded environments, and can locate mates with relatively high success rates. This suggests the presence of powerful strategies to deal with the transmission, detection and recognition of relevant signals. To avoid acoustic competition due

to the effect of masking interference, animals partition the acoustic resource in the temporal, spatial and spectral domains. Closely related species tend to be physically and behaviourally more similar than distantly related species, and are likely to possess similar songs and singing behaviour. The relationship between phylogenetic relatedness and trait similarity is investigated by quantifying what is called the 'phylogenetic signal'- the tendency of related species to resemble each other more than is expected by chance. As a result, acoustic interference is likely to occur more often among closely related species, and they may evolve divergent signals to compensate.

Drongos (Dicruridae) are a group of highly vocal passerines known for their vocal plasticity. There is a great extent to which their vocal repertoire can range in terms of diversity and function. Apart from having a wide range of species-specific repertoire, drongos are also mimetic species known to mimic the calls of conspecifics as well as other animals present in their environment. This study, conducted in Dehing Patkai Wildlife Sanctuary, Assam, focused on the four species of sympatric drongos- the Hair-crested Drongo, Lesser Racket-tailed Drongo, Greater Racket-tailed Drongo and Bronzed Drongo- and how they partition their acoustic niche. The study also looks into the ecological adaptations to counteract the impact of masking interference by habitat and closely related congeners. Active acoustic recording was done to record the four species of drongos in the study area. Line transects were walked along trails to calculate the density of each drongo species. Passive acoustic recorders were used to study the vocal activity patterns in the drongos. The study found evidence of overlapping acoustic niche between the drongos. However, they were significantly different from each other in the individual acoustic parameters. The drongos also occupied separate height classes, barring the lesser racket-tailed and the greater racket-tailed drongo. However, the drongos did not separate in their vocal activity pattern, suggesting overlap in the diel pattern. The study thus gives insight into the acoustic space of a group of highly versatile bird as well as the strategies they adapt to avoid interfering each other and thus co-exist.

3 INTRODUCTION

A lot of interest in the field of ecology revolves around how species that are closely related co-exist, and what governs this pattern (Gotelli and Albrecht 2001). Character displacement, or the difference in any trait characteristic among species present in sympatry, and the loss of it in entirety in parts where they do not overlap in range has been suggestive as a way by which closely related species can co-exist (Wilson and Brown 1955; Grant, 1972). as a selective force, allowing species with similar phenotypes to coexist. The competitive exclusion principle states that species that are ecologically similar cannot co-exist and will either go extinct or develop diverging traits, the concept of environment filtering regards the environment (Kraft et al., 2015). Considerable research has gone to understand how various traits of species living in sympatry allow them to coexist, and the evolutionary patterns of these traits.

Patterns of trait divergence vary depending on whether the species occur in sympatry or in allopatry. Sympatry is defined as the co-occurrence of more than one species in the same geographical area with overlapping ranges. If closely related species occur in sympatry, competition is likely to shape divergence in their ecological as well as in the sensory domain (example, acoustic signals(Krishnan & Tamma, 2016)). While ecological divergence can aid in utilizing different resources, acoustic divergence can prevent masking between species as well as reduce hybridization by species recognition (Seddon 2005).

Diverse animal taxa employ acoustic signals for a variety of functions including mate choice, species identification, resource defence and other ecological and social functions (Bradbury and Vehrencamp 1998). Birds are no exception. Birds use vocalization for a wide range of functions, including territory defence, mate attraction, resource defence (Catchpole and Slater 1995) as well as other social functions like kleptoparasitism, forming and associating with heterospecific flocks, raising alarm against predators, etc (Marler and Slabbekoorn 2004; Goodale 2006). Acoustic traits are of particular importance in habitats like forest where other traits like visual cues are not as effective in communicating and locating species, owing to dense vegetation and limited visibility (Catchpole and Slater 1995). Temporal partitioning is a way by which animals can ensure they do not compete with each other over an acoustic space (Brumm and Slabbekoorn 2005; Greenfield 1988.) This is particularly relevant in areas where multiple individuals of the same species, as well as multiple species, reside. Dawn choruses, for example, is a crucial time for birds to vocalise simultaneously, in the presence of other vocalizing members, in a very busy and crowded acoustic channel (Catchpole and Slater 1995). The fact that they do so without masking each other is suggestive of strategies to ensure there is no overlap in when they are singing. This is particularly important where two species have similarities in their song structures, and are phylogenetically related.

The primary aim of an acoustic signal is to efficiently communicate information over relatively long distances. This information, however, is subjected to changes and distortions imposed by the physical structure of the habitat, as well as masking interference from co-occurring signals of other acoustically communicating species (Brumm and Slabbekoorn 2005; Luther 2009). The natural habitat in which an animal calls can have significant effects on their signals and communication systems. Signals are attenuated due to spreading loss whereas reflection and scattering of sound by the ground and vegetation can lead to temporal pattern distortion and frequency filtering of the signal, thus compromising detection and recognition by receivers. (Schmidt and Balakrishnan 2014). Acoustic masking interference from background noise also decreases the efficacy of intraspecific communication by affecting the detectability and discriminability of conspecific signals (Endler 1992; Wiley 1994). Background noise from both biotic and abiotic sources is ubiquitous in natural environments (Luther 2009). This is exemplified by noisy dusk choruses consisting of several species of acoustically signalling insects, avian dawn choruses, frog choruses, conspecific flocks of birds etc, at the same time and place. Masking interference by background noise or the simultaneously vocalization of other species- especially ones closely related- incur several disadvantages to the vocalizing individual. Signals with similar features have a high potential of interference for the species vocalizing, as well as for the receiver interpreting it. These disadvantages- or costs- could be the failure to respond to appropriate signals and the unnecessary response to territorial or mating signals not meant for them. In fact, the problem exacerbates when closely related species make such errors, as it can lead to potential hybridization between species- a costly error. Studies have found growing evidences for closely related species in sympatry to have divergent vocalization to counter these effects. (Seddon 2005 for antbirds; Haavie et al. 2004 for flycatchers)

Separation in the spectral domain

A number of animals communicate successfully even in noisy and crowded environments, and can locate mates with relatively high success rates (Brumm and Slabbekoorn 2005). This suggests the presence of powerful strategies to deal with the transmission, detection and recognition of relevant signals. To avoid acoustic competition due to the effect of masking interference, animals partition the acoustic resource in the temporal, spatial and spectral domains. For example, using a slightly different frequency (pitch) enables frogs to accurately find mates even in a noisy cocktail party (Nityananda and Bee 2011). Several other studies have been conducted on anurans, including one by Chek et al. (2003) where he found 3 out of 11 anuran communities to partition in their spectral properties, e.g. dominant frequency. However, the majority of the communities did not show any acoustic partitioning, either because they separate their calls at the intervals of other species call, or there are enhanced receiver mechanisms, like a cryptic character displacement, that works to the benefit of the female frog receiving and perceiving the vocalization.

Vertical stratification as an adaptation to acoustic partitioning

Since the habitat of a species plays a role in shaping signal structures, it can also affect caller behaviour: senders of long-distance signals may be expected to select calling sites that maximise high-fidelity transmission (Endler 1993), and thus exhibit vertical stratification. After controlling for the effects of morphology, it was found that Antbirds were vocalizing at low frequencies in the understory and canopy and had higher frequencies in the more open midstory (Seddon 2005). This study also showed that most of the antbirds had a mean peak frequency in the range of 2-5kHz. This sound window is most effective to reduce degradation by reverberation. Although the results of this study were consistent with the hypothesis of the habitat having a role in the evolution of songs in different species, it failed to consider details of microhabitats, since the habitat classification was categorically placed into three classes: 1(<3m from the ground), 2(3-20m from the ground) and 3(over 20m). These categories failed to capture the nuances of the vocal traits in the different species of antbirds. On closer inspection, it was found that several understory and canopy species had high pitched loudsongs, while many mid-story species had lower pitched songs. One speculation for this is that songs may have evolved to optimise, and not maximise transmission, i.e. it may be beneficial for the song to degrade the further it goes if the receiver is near and going further may only bring attention from predators or parasites (Seddon 2005). Nemeth et al. (2001) conducted a propagation study to study the effects of song post heights on five sympatric antbird species. A song of a single species is adapted to a song post height if it shows a lower degradation of the signal compared to the same signal at other heights and relative to the overall pattern in degradation in other species (Reeve and Sherman 1993). The study found strong evidence of a selection for song post heights in 3 of the 5 species. That habitat can have an effect on song structure as well as divergence in related species is of even more importance when we consider how urban landscapes, and the associated noise level, may have an impact in the way birds communicate. In the Dutch city of Leiden, for example, a study on Great Tits revealed how these birds sang at a higher minimum frequency in noisy environments in order to avoid its masking by the predominantly low-pitched noise (Peet and Slabbekoorn 2003).

Temporal partitioning

Temporal partitioning is a way by which animals can ensure they do not compete with each other over an acoustic space (Brumm and Slabbekoorn 2005;

Greenfield 1988). This is particularly relevant in areas where multiple individuals of the same species, as well as multiple species, reside. Dawn choruses, for example, is a crucial time for birds to vocalise simultaneously, in the presence of other vocalizing members, in a very busy and crowded acoustic channel (Catchpole and Slater 1995). The fact that they do so without masking each other is suggestive of strategies to ensure there is no overlap in when they are singing. This is particularly important where two species have similarities in their song structures, and are phylogenetically related. A study by Cody and Brown (1969) using time series analysis showed how asynchronous the cyclic patterns of vocal activity was in two abundant species in the Californian Chaparrals, the wrentit and the Bewick's Wren. When the wrentit song was at a peak, the Bewick's wren song was at its lowest point. A study on the red-eyed vireo and the least flycatcher by Ficken et al. (1974) showed how the flycatcher avoided beginning a song while a vireo was vocalizing, again suggesting strategies to avoid competition for an acoustic space. Several other evidences exist from works on white-throated sparrows, ovenbirds and red-winged blackbirds (Wasserman 1977; Smith and Norman 1979). However, it is also interesting to note that there are also species which, far from avoiding overlap, tend to consistently attempt to overlap their rival's songs. A study on nightingales by Hultsch and Todt (Hultsch and Todt 1982) found interesting observations of attempted overlap with rivals as well as no effort to adjust their vocal activity timing to that of other males.

Phylogenetic signal in acoustic traits

Phylogenetic constraints on sound production mean that assemblages of close relatives are more likely to encounter a "cocktail party" situation when communicating to conspecifics(Bee & Micheyl, 2008) This is because closely related species tend to be physically and behaviourally more similar than distantly related species, and are likely to possess similar songs and singing behaviour (Luther 2009). Interest in this idea has taken shape ever since Darwin put forward the idea that "…species of the same genus have usually, though by no means invariably, some similarity in habits and constitution...". The relationship between phylogenetic relatedness and trait similarity is investigated by quantifying what is called the 'phylogenetic signal'- the tendency of related species to resemble each other more than is expected by chance (Blomberg and Garland 2002). This would occur if traits evolved in a Brownian motion-like manner, in which the amount of change is small and has a random direction.

As a result, acoustic interference is likely to occur more often among closely related species, and they may evolve divergent signals to compensate (Luther 2009 for birds, Kingston and Rossiter for bats, Schmidt et al 2011 for crickets, Narins 1992 for frogs). Passerine birds in particular, owing to vocal learning and mimicry, are highly vocally plastic, and have been relatively little studied in this regard. However, they pose interesting possibilities because of this, as this plasticity expands the range of possible behavioural and physics-based strategies they may employ to "get the message across" in an acoustically crowded environment.

Rationale of the study

Drongos (Dicruridae) are a group of highly vocal passerines known for their vocal plasticity. There is abundance of literature which describes the extent to which their vocal repertoire can range in terms of diversity and function (T. Flower, 2011; T. P. Flower, Gribble, & Ridley, 2014; Goodale & Kotagama, 2006; S. H. K. Satischandra, Kodituwakku, Kotagama, & Goodale, 2010). Apart from having a wide range of species-specific repertoire, drongos are also mimetic species known to mimic the calls of conspecifics as well as other animals present in their environment (Ali 1943; Ali and Ripley 1983).

Dehing Patkai Wildlife Sanctuary and the adjoining Jeypore Reserve Forest is situated in Northern Assam, India. In the study area, there are four species of sympatric drongos, viz. *Dicrurus paradiseus, Dicrurus aeneus, Dicrurus remifer and Dicrurus hottentottus.* These drongos are known to use vocalization for similar social functions. Additionally, the study area is highly biodiverse with high number of vocally communicating species (http://ebird.org). In this comparative study of four sympatric drongo species, we aim to understand the acoustic partitioning in sympatric drongo assemblage in Dehing Patkai Wildlife Sanctuary, i.e. how each species of drongo maintains a distinct acoustic niche. The study aims to investigate phylogenetic signal in the acoustic traits of drongos, as well as the ecological strategies used by drongos to counteract the masking interference by habitat and closely related congeners.

4 OBJECTIVES AND RESEARCH QUESTIONS

Objective 1.

- **To assess the acoustic trait patterns in sympatric species of drongos**
- *Do the four species of drongos, occurring in sympatry, exhibit divergent acoustic signals?*
- *Do drongos exhibit different/similar acoustic signals due to their phylogenetic relatedness?*

AND

Objective 2.

- **To understand the ecological strategies of drongos to differentiate their niches, with special reference to their auditory niches.**

- *Are the different drongo species present in different abundances?*
- *Are the different drongo species calling from different song perch heights?*
- *Are the different drongo species calling at different times of the day-temporal partitioning?*

5 METHODS

5.1 Study Area

The study was conducted in Dehing Patkai Wildlife Sanctuary and adjoining Jeypore Reserve Forest (27°16'46.68"N, 95°29'32.91"E), in the Jeypore range of the Dibrugarh Forest Division in the state of Assam, India from December 2018 to April 2019 Figure 5-*5-1*. The sanctuary covers an area of 111.19sq. km. The vegetation is classified as Assam Valley tropical evergreen forest (category 1B/C1) (Champion and Seth 2013), and is also part of the Dehing Patkai Elephant Reserve. The sanctuary is the last stronghold of tropical lowland evergreen forests in the country. Important species of flora include *Dipterocarpus artocarpus* (Hollong), *Shorea assamica* (Mekai), *Dillenia indica*, *Mesua ferrea*, *Myristica limifolia*, *Castanopsis indica*, etc.

The sanctuary, owing to its unique biogeographical history, has a wide diversity of fauna. 47 species of mammals, including Hoolock Gibbons, Pig-tailed Macaque, Stump-tailed Macaque, Slow Loris, Clouded Leopard, Marbled Cat, Golden Cat, Binturong, Spotted Linsang, etc occur here. In addition to this, the sanctuary is also home to around 300 species of birds. The protected area also supports a variety of lesser fauna, which include numerous varieties of insects, including butterflies, grasshoppers, moths and beetles; reptiles, fishes and other lesser life forms (Kakati 2004).

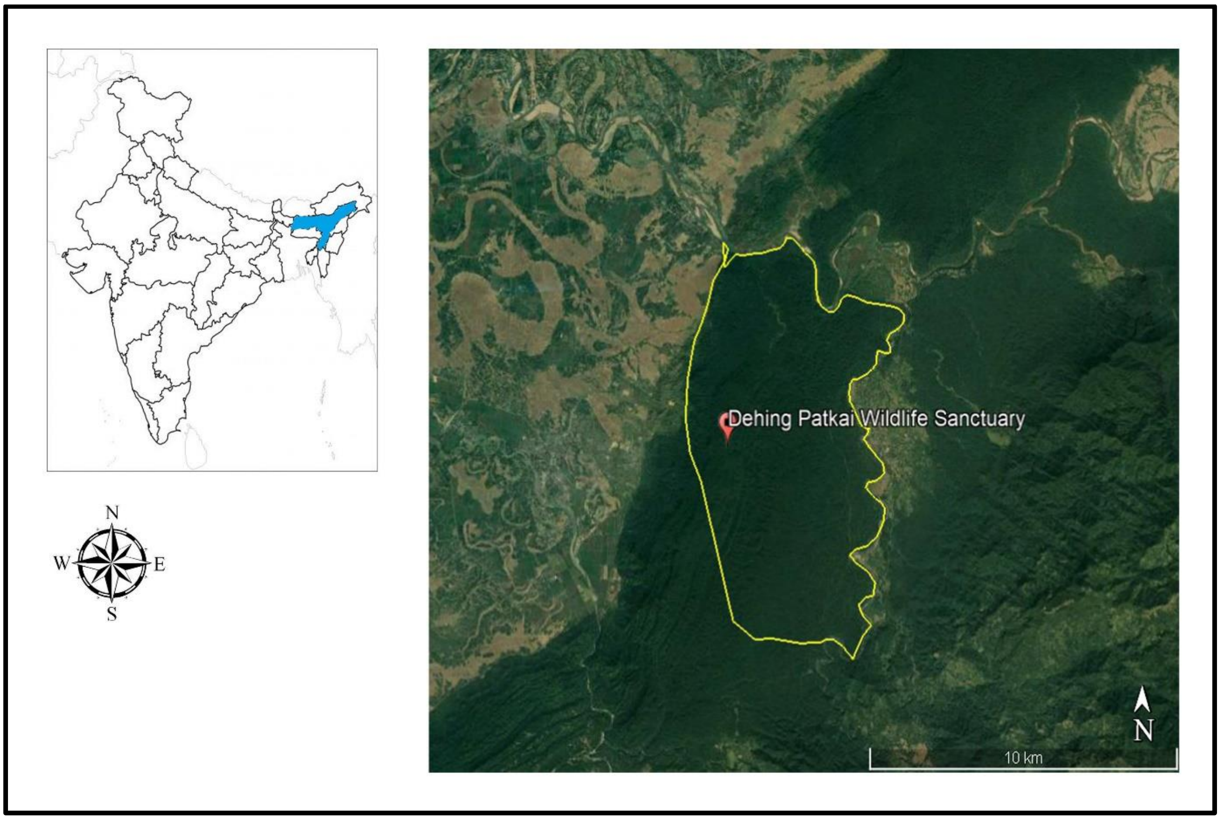

Figure 5-5-1 Map of the study area

5.2 Study Species

The study focused on drongos (Aves: Dicruridae), an insectivorous passerine. Of the 29 species of drongos belonging to the genus *Dicrurus*, 10 species occur in India (Grimmett et al. 2013). They are tree-dwelling, medium sized birds known for their diverse vocal repertoire, capable of plasticity through mimicry of other species (Ali and Ripley 1983). Of the 10 species in the country, seven species occur in my field site; *D. paradiseus (*Greater Racket-tailed Drongo*), D. aeneus (*Bronzed Drongo*), D. remifer* (Lesser Racket-tailed Drongo)*, D. hottentottus* (Hair-crested Drongo*), D. adsimilis* (Black Drongo*), D. leucopheus (*Ashy Drongo*) and D. annectans (*Crow-billed Drongo*)* (Grimmett et al. 2013). However, the study focused on only four species- Greater Racket-tailed Drongo, Bronzed Drongo, Lesser Racket-tailed Drongo and Hair-crested Drongo. The Black Drongo is not found in sympatry with the other species; the Ashy Drongo, a winter migrant, was found in low number and never vocalized; and the Crow-billed

Drongo, a possible summer migrant was encountered very rarely during the end of the field work. Hence, I did not collect data from these species.

The Greater Racket-tailed Drongo *Dicrurus paradiseus* is the largest drongo found in the Indian Subcontinent. It is readily identified by its extremely long tail streamers- or rackets- giving the species its name. in India, it is found throughout the foothills of Himalaya, large parts of central India and into the Western and Eastern Ghats. Its range, however, extends all the way to Borneo and Java (Ali and Ripley 1983). The Greater Racket-tailed Drongo is an exceptional mimic, with numerous species being mimicked by it. JC Daniels, in a paper in J. BNHS, reports the drongo mimicking not just the alarm call of the Jungle Babbler but also mimicking the alarm calling behaviour of the babbler. Several others report the bird to extend its vocal repertoire to include multiple species, including frogs, insects, mammals and even sounds like mobile ringtones. The Greater Racket-tailed Drongo is mostly found individually or in pairs, often in a mix species flock. Studies in Sri Lanka have found out how they use their vocalizations to form mix flocks (Goodale 2006; Satishchandra 2010)

The Lesser Racket-tailed Drongo *Dicrurus remifer* is a large drongo found in the north and north-eastern parts of our country. Largely insectivore, the drongo also has two long, extending tail feather- or rackets- but they are simply oval in shape unlike the more intricate racket of the *D. paradiseus*. They have a wide vocal repertoire, and also actively take part in mix flocks. (Ali and Ripley 1983)

The Bronzed Drongo *Dicrurus aeneus* is a small-sized drongo found singly or in groups of 2-4. They are found in the Western and Eastern Ghats as well as in the North and North-eastern states. Their range extends all the way to South-east Asia. An insectivore, the Bronzed Drongo often takes part in mixed flocks in or near the forest canopy (Ali and Ripley 1983).

The Hair-crested Drongo *Dicrurus hottentottus* is a large species of drongo found in most parts of the subcontinent. Earlier treated as conspecific to the Spangled Drongo *Dicrurus bracteatus*, it is now a separate species. The Hair-crested

Drongo is primarily nectarivore and moves locally with the blooming of flowers of *Bombax ceiba, Erythrina*, etc. They are noisy and are found in small groups (Ali and Ripley 1983).

5.3 Data Collection

Abundance estimation

To estimate the abundance of each species of drongo, I walked line transects. Because of the difficulty in access in many parts, as well as the inability to cut random transects, existing trails were used as transects. There were 6 major trails in the study Figure 5-2, which consisted of 26 transects in total *Table 5-1*. Each transect had a length of 1km. from a brief recce in December 2018, I observed peak bird activity between 7am to 10am and between 1pm to 3:30pm. Thus, I repeated the transects both in the morning as well as in the afternoon, as temporal replicates, and each trail was repeated 2-3 times to increase detection. The morning transects began at 7am during winters and at 6am during summer as the day began earlier in summers and so does the activity period. The afternoon transects began at 1pm. During each walk, whenever a bird was encountered, I recorded the distance from my point, the trail bearing, the animal bearing, the number of individuals. For drongos, I additionally noted the GPS point, the perch height and note on whether it was calling or not.

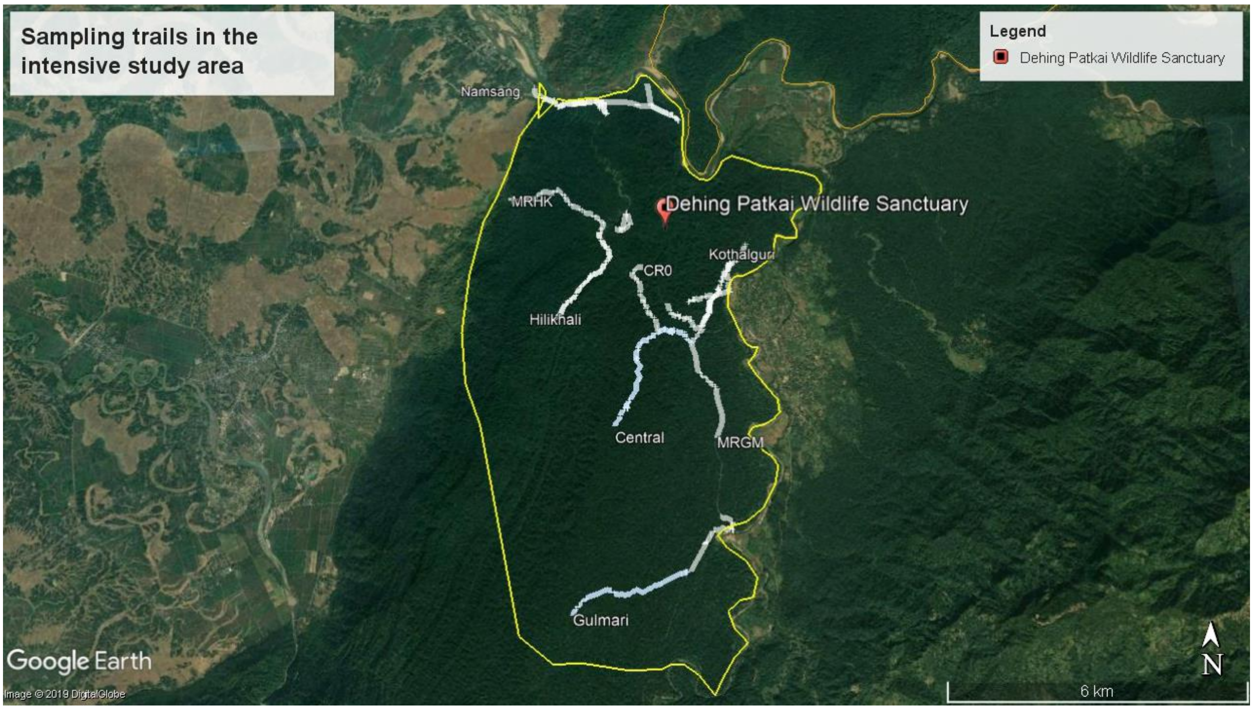

Figure 5-2 Sampling trails in the intensive study area in Dehing Patkai Wildlife Sanctuary, Assam, India

Table 5-1 List of sampling trails, transects in each trail and the transect lengths

Number	**Trail**	**Transect ID**	**Transect length**
1	Central	CR0	1000
2	Central	CR1	1000
3	Central	CR2	1000
4	Central	CRSC	500
5	Central	HapK1	1000

6	Central	HapK2	1000
7	Kothalguri	KG1	1000
8	Kothalguri	KG2	1000
9	Kothalguri	KG3	1000
10	Kothalguri	KGRight	330
11	Hilikhali	HK1	1000
12	Hilikhali	HK2	1000
13	Hilikhali	HK3	1000
14	Hilikhali	HKHalf	500
15	Namsang	NS1	1000
16	Namsang	NS2	1000
17	Namsang	NS3	1000
18	Namsang	NS4	1000
19	MRGM	MRGM1	1000
20	MRGM	MRGM2	1000
21	MRGM	MRGM3	1000
22	MRGM	MRGM4	1000
23	MRGM	MRGMR1	400
24	MRHK	MRHK1	1000
25	MRHK	MRHK2	1000
26	MRHK	MRHK3	1000

Phylogenetic Signal

To detect phylogenetic relatedness in traits, I tested for phylogenetic signal of acoustic parameters. For this, I adapted the phylogenetic tree from Pasquet et al., 2007, where the world drongo phylogeny was built. I first sourced the calls of all the drongo species found in the world, particulary those depicted in the tree. These recordings were sourced in the .wav format from AVoCet (https://avocet.integrativebiology.natsci.msu.edu/) as well as Macaulay Library (https://macaulaylibrary.org) of Cornell University. I digitized these recordings and extracted the same parameters used for my active recordings.

As each of these species had recordings of several individuals, I compiled all the parameters and averaged (both arithmetic and geometric) the values of each parameter, to be used for the analysis.

Active sound recording

To record the different species of drongos, I walked trails and transects in my field site during mornings and afternoons when the activity period of birds was high. When a drongo was detected, I used a digital audio recorder (Zoom H4n) along with a Sennheiser ME66 unidirectional microphone with a K6 power module to record the vocalization of the individual. While recording, I also took notes of the perch height, the context of the vocalization and the presence or absence of other species. I recorded the drongo for as long as they were within visible range. I took care to record only when I see the drongo in order to prevent any misidentification of calls, as they can be very confusing and also because there are other birds like the Blue-winged Leafbird *Chlorpsis cochinchinensis* and the White-rumped Shama *Copsychus malabaricus* which have a tendency to accurately mimic drongos. I also recorded the GPS location for each recording.

Perch height

To understand whether drongos select different perch heights, I recorded perch heights whenever I encountered a drongo. I estimated the height by a combination of both clinometer (Suunto Tandem/360PC/360R DG clino/compass) as well as ocular estimation. These recordings were done whenever I sampled for acoustic recording, during transect walks, during vegetation sampling, or any ad libitum sighting of drongos. I also noted down whether the drongo was calling at that perch or not.

Vocal Temporal Activity

In order to understand whether the different drongos call at different times of the day, I used a combination of both active as well as passive recording as well as *ad libitum* records. Whenever a drongo was encountered, I noted down the time when they were seen calling. To reduce the sampling bias, I also used passive acoustic recorders-AudioMoth. The AudioMoths were deployed in various locations (n=15) Figure 5-3 in four of my sampling trails. The other two trails were not used as there was human traffic and thus a possibility of recorders being stolen. They were programmed to record at a sampling rate of 16KHz, and were left to record for 24 hours. Each AudioMoth recorded for 5 minutes followed by 1 minute of sleep. Each AudioMoth was placed at a distance of ~500-600m away from each other to avoid detecting the same individuals in two or more recorders.

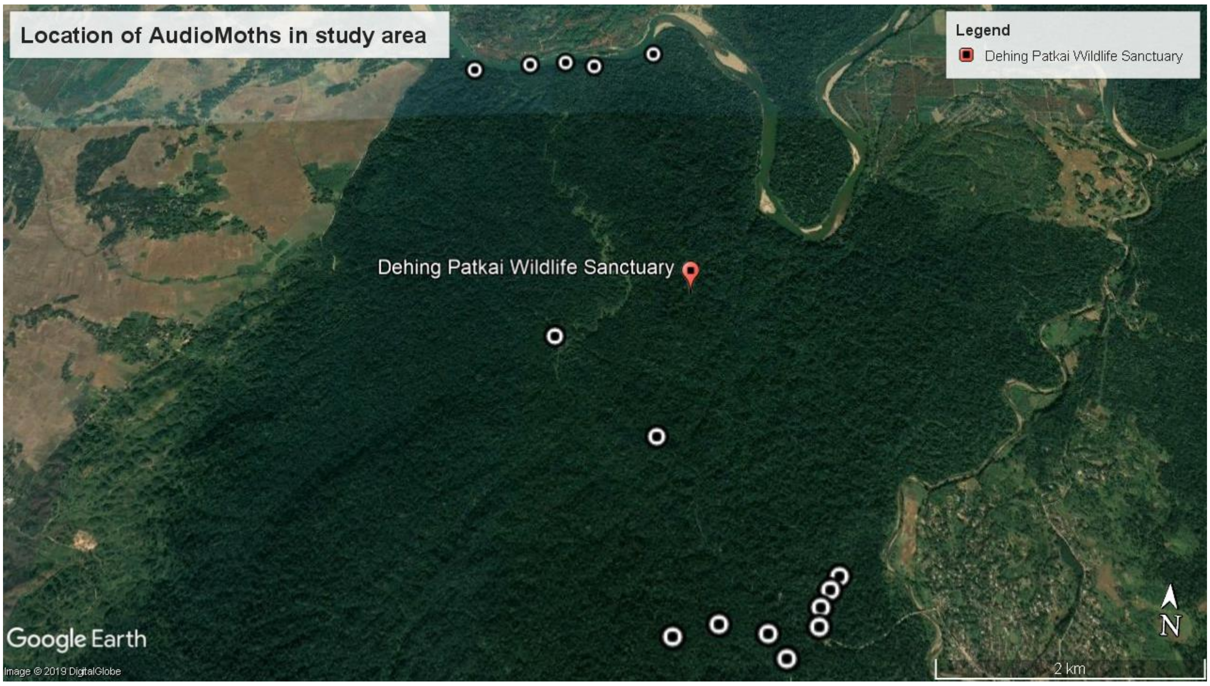

Figure 5-3 Location of Audiomoths in the study area. The audiomoths were placed in the sampling trails, where I had regular encounters of higher number of individuals of drongos.

5.4 Analytical Methods

Abundance estimation

I used DISTANCE 7.3 software (Buckland et al. 2001) to estimate the density/km^2 of the four species of drongos in the study area. The densities were calculated trail wise, with each trail having multiple line transects. I also calculated overall density of each drongo in my study area.

Phylogenetic signal

I calculated Blomberg's K (Blomberg et al. 2003) for each acoustic trait to understand the patterns of phylogenetic signals. This analysis helps to understand whether the patterns observed in our acoustic traits are a result of a common ancestry, i.e.- species that are closely related are more similar in their traits. We also calculated Pagel's λ (Pagel 1990), another parameter to estimate phylogenetic signal in traits. The value of λ lies in between 0 to 1, with value close to 0 indicating no phylogenetic signal, while a value close to 1 indicates presence of phylogenetic signal in the trait. Both Blomberg's K and Pagel's λ were calculated for all acoustic signal traits. The analyses were done using package 'phytools' (Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things) in the R software.

Acoustic Analysis

I first digitized all the recordings in the software RAVEN PRO 1.5.0 (www.birds.cornell.edu/raven). RAVEN generated spectrograms of the recordings. Following this, each of the notes Figure 5-4 were digitized by drawing a selection table on them-labelling. To select only notes and exclude any echo, it is important to listen to the note in low speed to visually understand where the note starts and where it ends. This is a necessary caution that has to be taken to ensure we do not draw a selection box over the echo of the note. By labelling each note, RAVEN generates sound parameters for each individual note. The song parameters to be generated can be added manually.

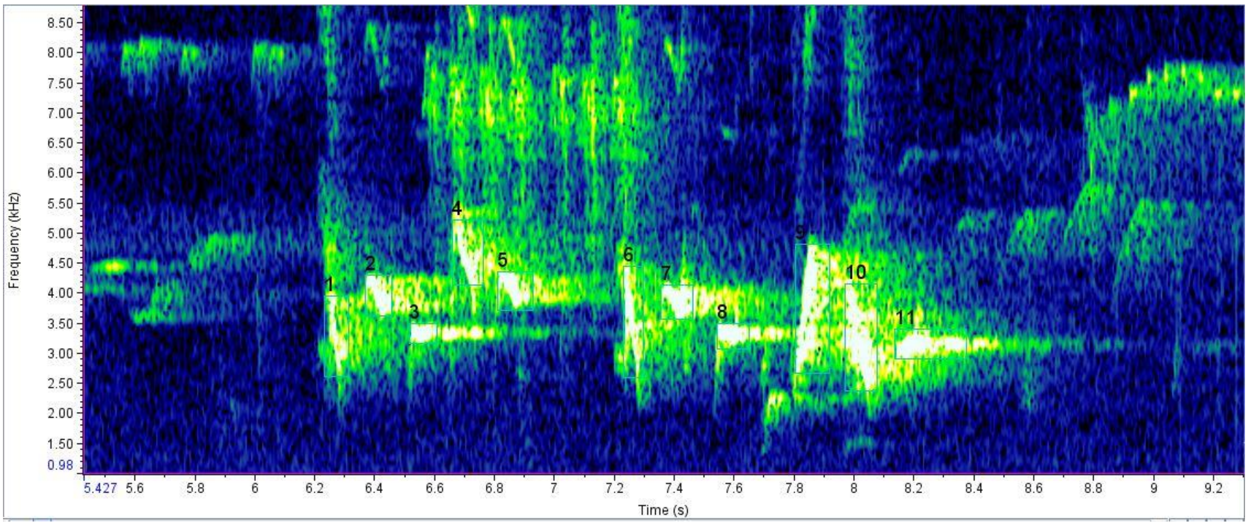

Figure 5-4 Digitizing notes on RAVEN PRO 1.5.0. Each note is digitized by drawing a selection box (labelling)

Following digitization, I used 9 variables/song parameters for final analysis, which were generated for each note by the software. A description of each note is present in the following table Table 5-2

Table 5-2 Description of acoustic parameters used to compare across species

Acoustic Parameter	Description
Peak Frequency	The frequency at which maximum power/frequency occurs in the given selection.
Average entropy	A measure of how fuzzy or clear (tonal) the selection is. It gives a measure of the disorder in a sound selection.
Peak time relative	The time at which the peak amplitude occurs in the selection.
Delta time	The difference between begin time and end time of the selection.
PFC max	Maximum of the peak frequency contour (the peak frequency from each spectrogram slice of selection).
PFC Min	Minimum of the peak frequency contour (the peak frequency from each spectrogram slice of selection).
Start frequency of Peak frequency contour (PFC)	The first peak frequency measurement of the peak frequency contour.
End frequency of Peak frequency contour (PFC)	The last peak frequency measurement of the peak frequency contour.
Bandwidth @ 90%	The bandwidth at which 90% of the energy is concentrated.

I first classified each note as mimicry and species-specific. By virtue of a drongo's vocal plasticity and their ability to learn vocalization, mimicry in species increases the versatility of the species and can likely confound any analysis to compare species trait, I used only species-specific notes for the final analysis. Notes termed as 'Mimicry' were adjudged based on my knowledge of calls of other birds, as well as cross-checked with other people to confirm. To look for how separate the vocalizations of the four species of drongos are in a multidimensional space and which parameter contributes most to the variation between them, I used Principal Component Analysis (PCA) on the 9 song parameters. PCA is a statistical analysis used to find out which parameters contribute the most to the variation that is observed. The PCA was done on a correlation matrix. A correlation matrix is used if the units of measurements of the individual variables differ.

Then, I plotted the acoustic variables that explains the most variation in the PCA as box plots to explore variability in the data, following which statistical significance tests were done. The first test was an Analysis of Variance (ANOVA) test to check for overall difference of acoustic traits between species. Following this, I conducted a Tukey’s honestly significant difference test to see pair-wise patterns of differences. I also plotted the variables as density plots, followed by a pairwise KS test to check for significant difference between pairs of species (Crawley 2012). The analyses were done in R software (R 3.6.0).

The plots revealed variation in each acoustic parameter when compared across species. Given the variability in the acoustic parameter distributions and due to lack of context available for the vocalizing individuals of drongos, I used the data from the 25th to 75th quartile range. This is the most frequently used parameter range that the drongo uses. I plotted the data and ran a one-way ANOVA followed by Tukey’s HSD test on this data set.

Perch Height

To look for difference in perch heights, I first plotted the perch heights as box plots for each species. The plots were made for only heights where I observed the bird calling (noted as calling perch). I conducted a one-way ANOVA test to check for differences in the means between species, followed by Tukey’s Honestly Significant Difference (HSD) test for a pairwise comparison. All the analyses were done in R. (R 3.6.0).

Temporal Vocal Activity Pattern

Vocal activity was noted for each individual encountered vocalizing. From the active recordings, I noted the time at which they vocalized. If the recordings exceeded a minute, I took a second note of time.

From the passive recordings, I subsampled my entire dataset as follows: Each hour of recording had ten 5-minute recordings (each 5-min recording is henceforth referred to as ‘sample’), totalling 50 minutes. An hour was divided into 20-minute ‘segments.’ Each 20-minute segment contains 3 ‘samples’, from which I used the first two sample. This not only reduced processing time but also ensured full coverage of the entire hour. These samples were visualised in RAVEN PRO 1.5.0. I then listened to the samples and noted down the time when a drongo species vocalized *Figure 5-5*.

Following this, I calculated the number of vocal activities in each hour of the day, for each species. This was plotted as a line graph to visualise the differences in vocal activity pattern. The overlap in vocal activity pattern was calculated using package overlap in R (R 3.6.0).

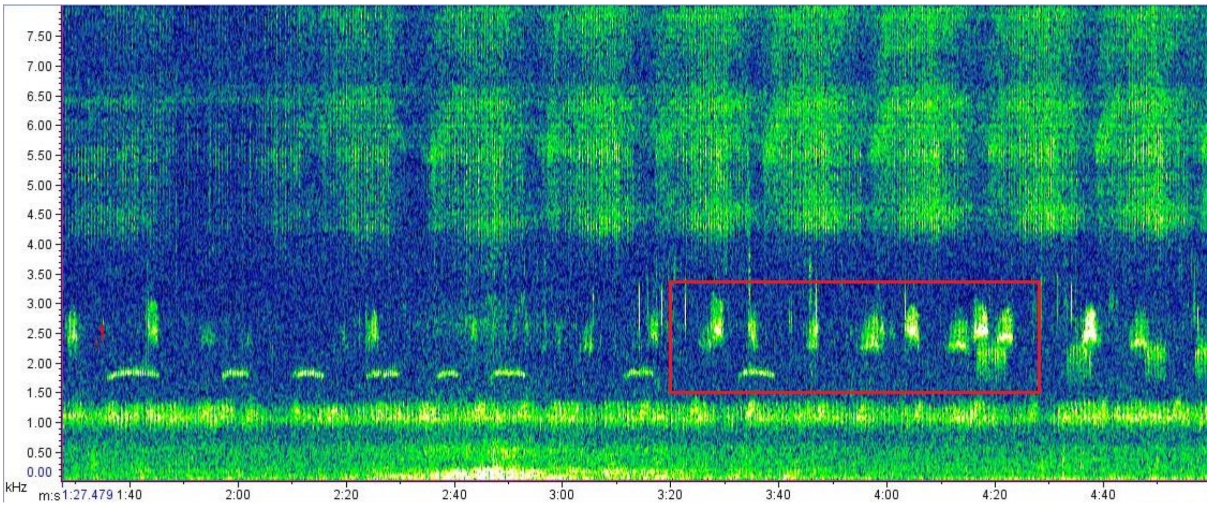

Figure 5-5 Spectrogram of a ‘sample’ visualised in RAVEN Pro. with a Greater Racket-tailed Drongo detected.

6 RESULTS

6.1 Density estimation

In the study area, Bronzed Drongos were highest in density (37.53/km^2), followed by Lesser Racket-tailed Drongo (10.24/km^2), Greater Racket-tailed Drongo (7.03/km^2) and the lowest being the Hair-crested Drongo (5.73/km^2). The results are summarised for total densities of each drongos (Figure 6-1;Table 6-1).

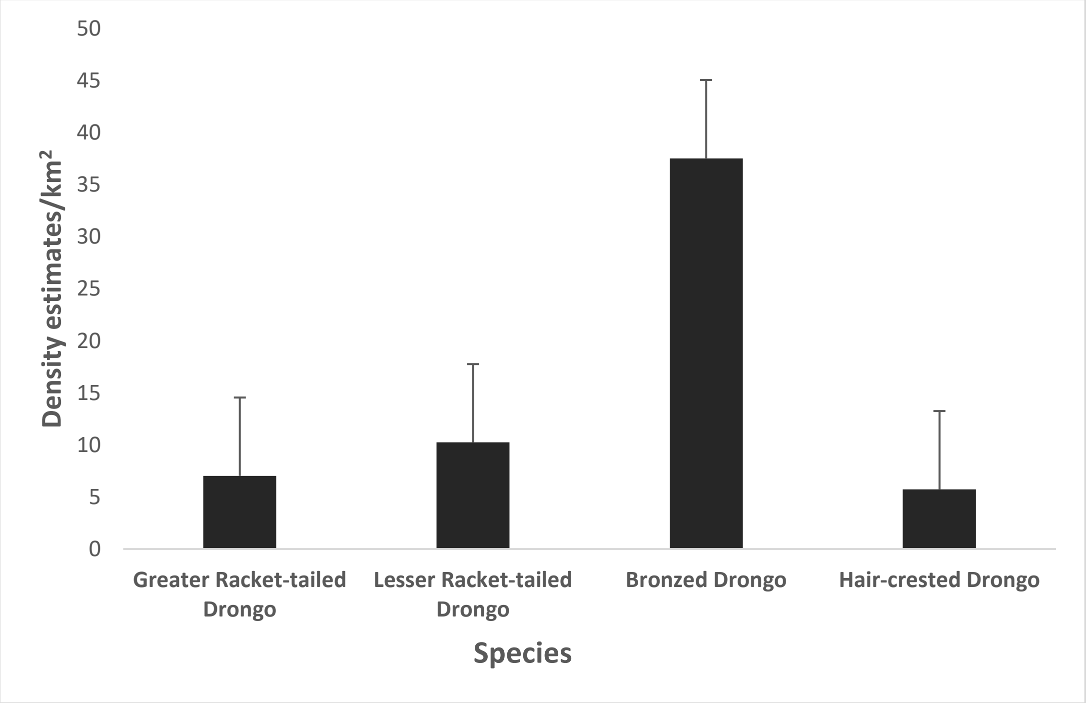

Figure 6-1 Densities of drongos in study area. From left to right: Greater Racket-tailed Drongo, Lesser Racket-tailed Drongo, Bronzed Drongo and Hair-crested Drongo

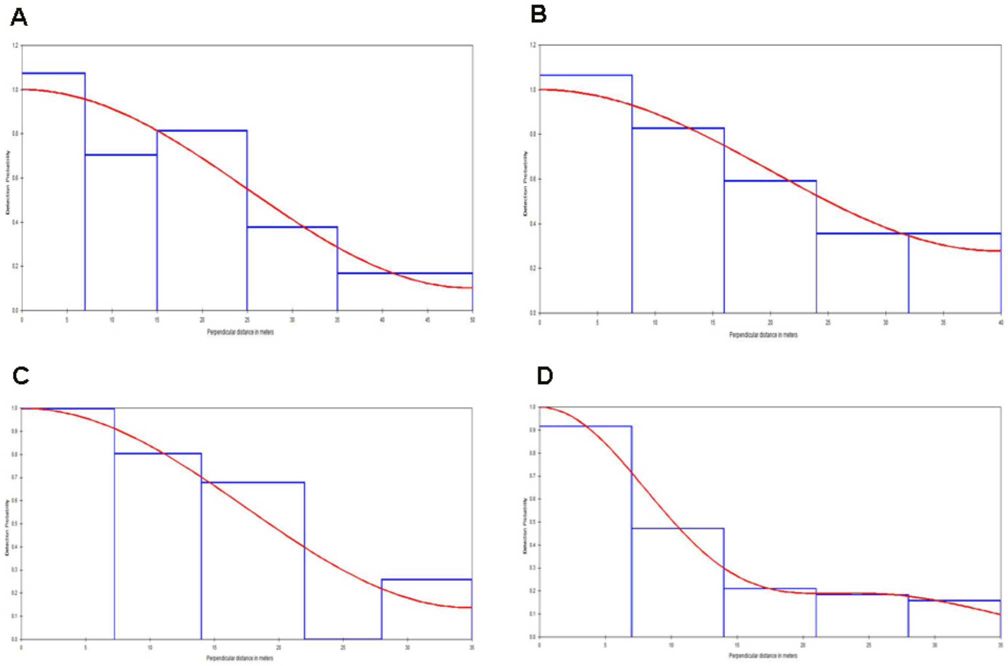

Figure 6-2 Detection probability graph for A- Lesser Racket-tailed Drongo; B- Greater Racket-tailed Drongo; C- Hair-crested Drongo and D- Bronzed Drongo

Table 6-1 Density estimates of Greater Racket-tailed Drongo, Lesser Racket-tailed Drongo, Bronzed Drongo and Hair-crested Drongo in the study area

Species	**Greater Racket-tailed Drongo**	**Lesser Racket-tailed Drongo**	**Bronzed Drongo**	**Hair-crested Drongo**
Total effort (metres)	79011	79011	79011	79011
Total number of individuals	27	44	74	11
Density/km^2	**7.03± 2.33**	**10.24±1.98**	**37.53±7.54**	**5.73±3.52**
%cv	33.19	19.38	20.1	61.46

Encounter Rate/km	0.03	0.06	0.01	0.001
Probability ofDetection	0.63**±0.09**	0.55**±0.05**	0.38**±0.040**	0.56**±0.1**
ESW (in metres)	25.33**±3.93**	27.53**±2.40**	13.55**±1.70**	19.88**±3.64**
Model	Uniform cosine	Uniform cosine	Half Normal Cosine	Uniform cosine
AICc	84.36	137.68	206.18	33.23
p-value	0.96127	0.7946	0.93654	0.94493

Densities were also calculated for each drongo species on each trail. The results are summarised in the table below Table 6-2. The Bronzed Drongo has the highest density in each of the trail. However, the Lesser Racket-tailed Drongo and the Greater Racket-tailed Drongo have different densities in each trail. The Hair-crested Drongo was detected in only three of the trails, and thus there are no density estimates of this species from the other trails.

Table 6-2 Densities of Bronzed Drongo, Greater Racket-tailed Drongo, Lesser Racket-tailed Drongo and Hair-crested Drongo on each trail

	Central	Hilikhali	Kothalguri	MRGM	MRHK	Namsang
Bronzed Drongo (/km^2)	43.63±18.9	80.91±25.78	33.92±10.56	27.56±13.56	35.35±14.73	26.05±12.68
Greater Racket-tailed Drongo (/km^2)	8.76±2.52	24.14±13.86	1.72±1.25	6.39±3.46	1.85±1.8	5.83±2.16
Lesser Racket-tailed Drongo (/km^2)	6.52±3.15	5.61±3.26	14.41±4.47	5.94±2.9	5.15±2.51	17.16±3.43
Hair-crested Drongo (/km^2)	0	24.46±15.22	3.48±3.84	3.2396±3.28	0	9.84±9.99

6.2 Phylogenetic patterns in acoustic traits

Before exploring the differences in acoustic traits, I explored the phylogenetic relatedness of each trait. This would help identify traits that are similar due to shared ancestry. Such traits need to be removed from further analysis, as any similarity or difference of these traits are not due to selective forces or adaptations, but purely due to shared ancestry. I calculated Blomberg's K Table 6-4 as well as Pagel's λ Table 6-3 for each of the acoustic traits. Both Blomberg's K and Pagel's λ were not significant. For all the acoustic traits, the value of Blomberg's K was close to 0, indicating that acoustic traits have much lower phylogenetic signal than is expected under Brownian motion. Similarly, Pagel's λ value of close to 0 also indicates less phylogenetic signal than expected, indicating a selective force acting upon these traits. Based on these results, all traits were explored for further analysis.

Table 6-3 Pagel's λ values for each trait

Trait	**Pagel's λ**	**p-value**
Average entropy	6.61E-05	1
Bandwidth @ 90%	6.61E-05	1
Peak Frequency	6.61E-05	1
Peak time	6.61E-05	1
Delta Time	6.61E-05	1

Table 6-4 Blomberg’s K values for each trait

Trait	Blomberg’s K	p-value
Bandwidth at 90%	0.1197273	0.7932068
Delta Time	0.1368436	0.8291708
Peak frequency	0.1230155	0.7892108
Peak time	0.137596	0.772
Average entropy	0.126661	0.79

6.3 Acoustic trait patterns

A summary of the total number of recordings of each species of drongo as well as the total number of notes extracted and digitized from them are given in *Table 6-5*.

Table 6-5 Summary of active recordings- number of recordings of each species and number of notes of each species digitized for analysis

Species	Number of recordings	Total number of notes digitized
Greater Racket-tailed Drongo	10	1248
Lesser Racket-tailed Drongo	30	1094
Hair-crested Drongo	11	235
Bronzed Drongo	33	936

Greater Racket-tailed Drongo

The Greater Racket-tailed Drongo is the largest species of drongo in the study area (Grimmett et al. 2013). It is characterised by its long wings, sharp crest and a diverse vocal repertoire *Figure 6-3*.

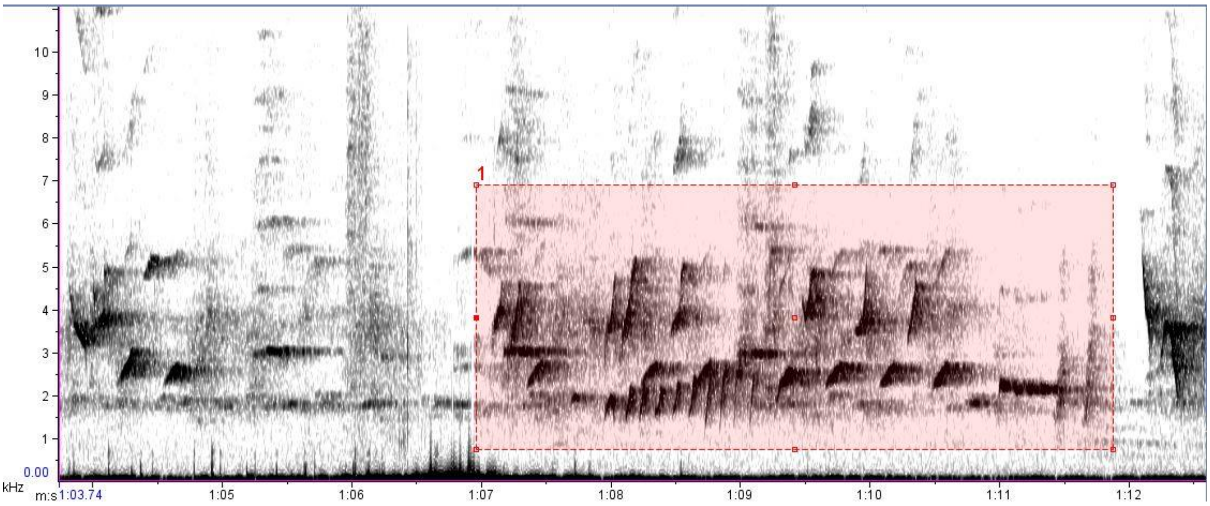

Figure 6-3 Spectrogram of a recording of the Greater Racket-tailed Drongo

Lesser Racket-tailed Drongo

The Lesser Racket-tailed Drongo is a mid-storey species of drongo, very similar in habits and morphology to the Greater Racket-tailed Drongo (Ali and Ripley 1983). The species has a diverse vocal repertoire, and is capable of mimicry *Figure 6-4*.

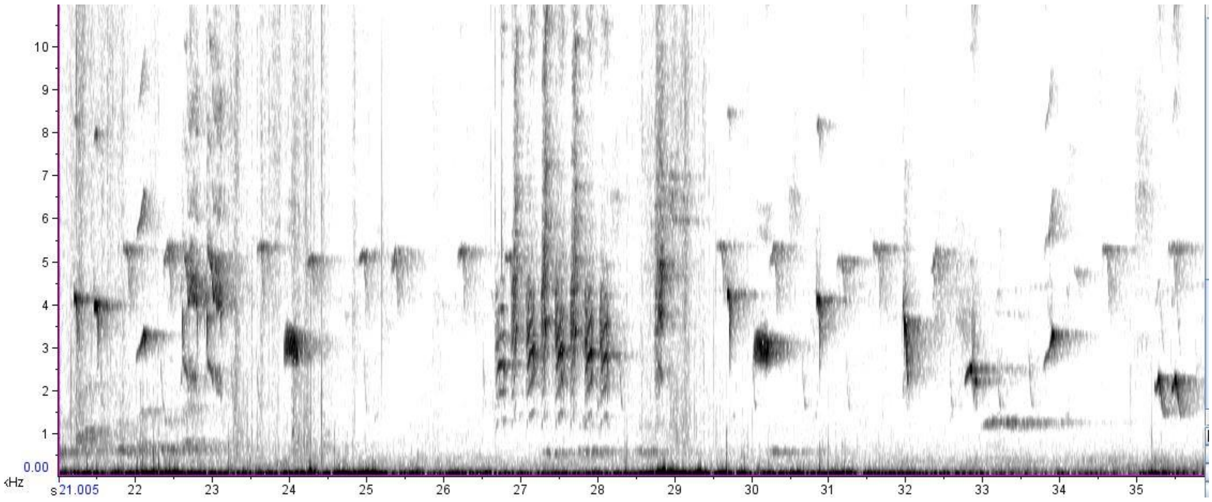

Figure 6-4 - Spectrogram of a recording of the Lesser Racket-tailed Drongo

Bronzed Drongo

The Bronzed Drongo is one of the smaller drongo species in the subcontinent. It is usually found in groups of two to four, and have a propensity to flock in the upper canopy with mix species flocks. They are also capable of mimicry *Figure 6-5*.

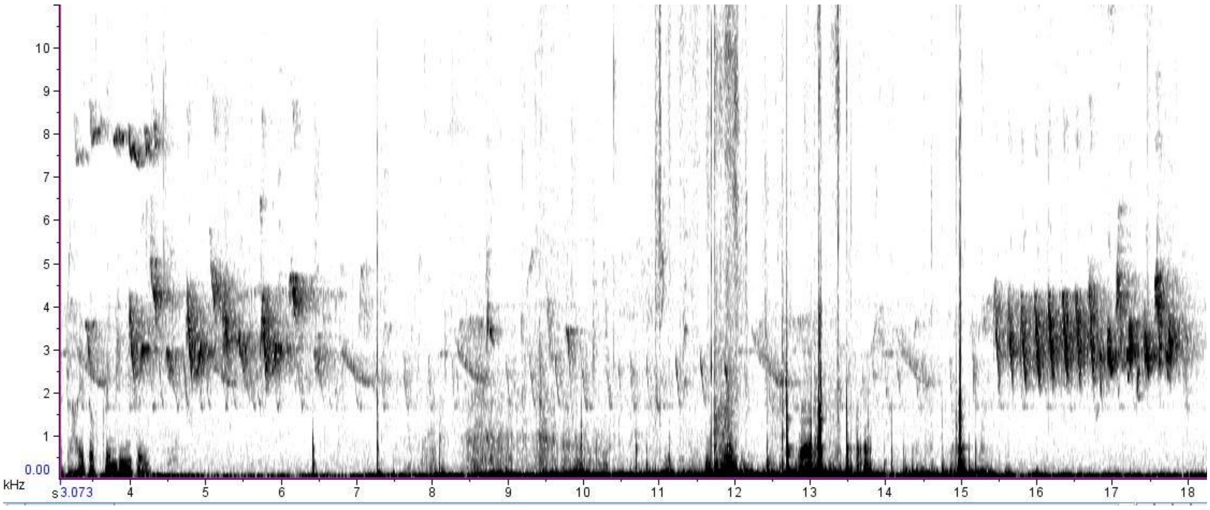

Figure 6-5 Spectrogram of a recording of the Bronzed Drongo

Hair-crested Drongo

The Hair-crested Drongo is a large drongo. It is primarily nectarivore and are known to gregariously forage on flowering trees like *Bombax ceiba, Erythrina*, etc. Unlike the other drongo species, the Hair-crested does not have a high vocal repertoire diversity as it has limited functions associated with its vocalization *Figure 6-6*.

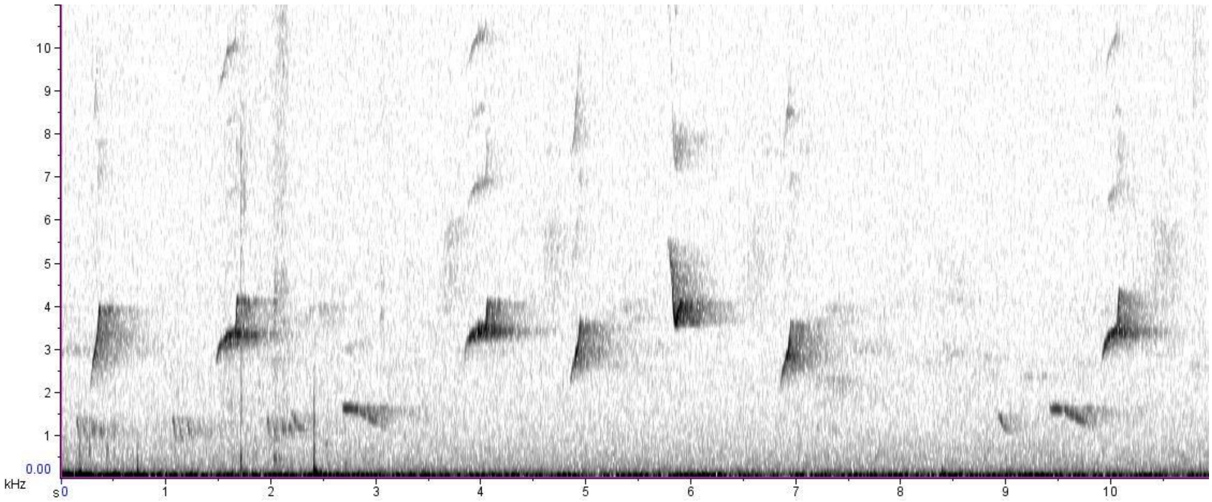

Figure 6-6 Spectrogram of a recording of the Hair-crested Drongo

Trait analysis

To understand how differently the four species of drongos vocalize in sympatry, we use principal components analysis. The first two principal components together explained 72.7% variation, while the first three principal components together explained 85.8% of the variation. The loadings and cumulative %variation is summarised in *Table 6-6*.

Table 6-6 Loadings of acoustic variables on principal components and cumulative %variation

Acoustic trait	PC1	PC2	PC3
Bandwidth @ 90%	0.249618	**0.635499**	0.034185
Delta Time (Seconds)	-0.05899	0.059989	**-0.69304**
Peak Frequency (KHz)	**0.425405**	-0.14446	-0.06531
PFC Max Frequency (KHz)	**0.440739**	0.052616	-0.08532
PFC Min Frequency (KHz)	**0.384342**	-0.37939	-0.03969
Peak Time Relative	-0.00234	0.190471	**-0.66731**
Average Entropy bits.	0.259913	**0.587002**	0.202574
1st frequency in the PFC(KHz)	**0.411214**	-0.14838	0.066855
Last frequency in the PFC(KHz)	**0.41787**	-0.14866	-0.12079
Standard Deviation	2.2236	1.2664	1.0866
Proportion of variance	0.5493	0.1781	0.1311
Cumulative proportion	0.5493	0.7275	0.8587

I then plotted the PC scores of PC1 and PC2 for both the data sets- both mimicry and species-specific notes *Figure 6-7*, as well as only species-specific notes *Figure 6-8*- for all four species of drongos.

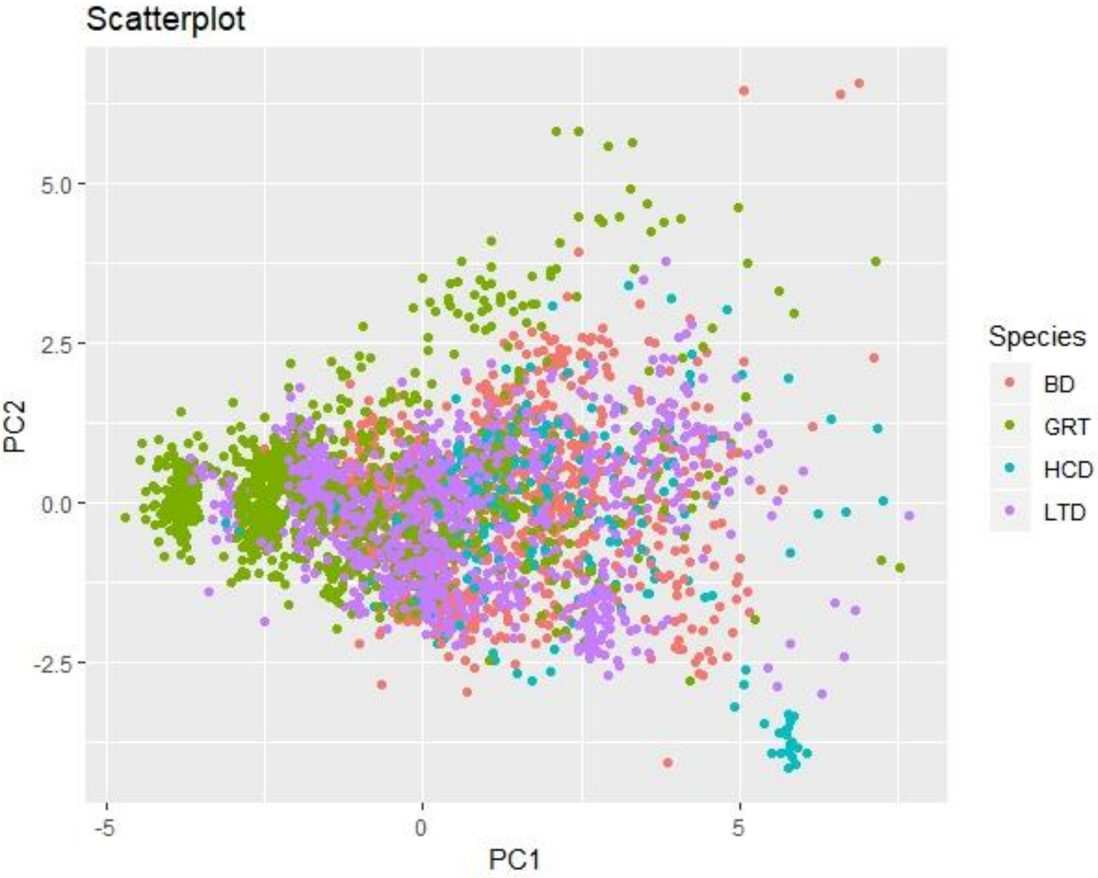

Figure 6-7 Plot of PC1 vs PC2 for both species-specific and mimicry notes

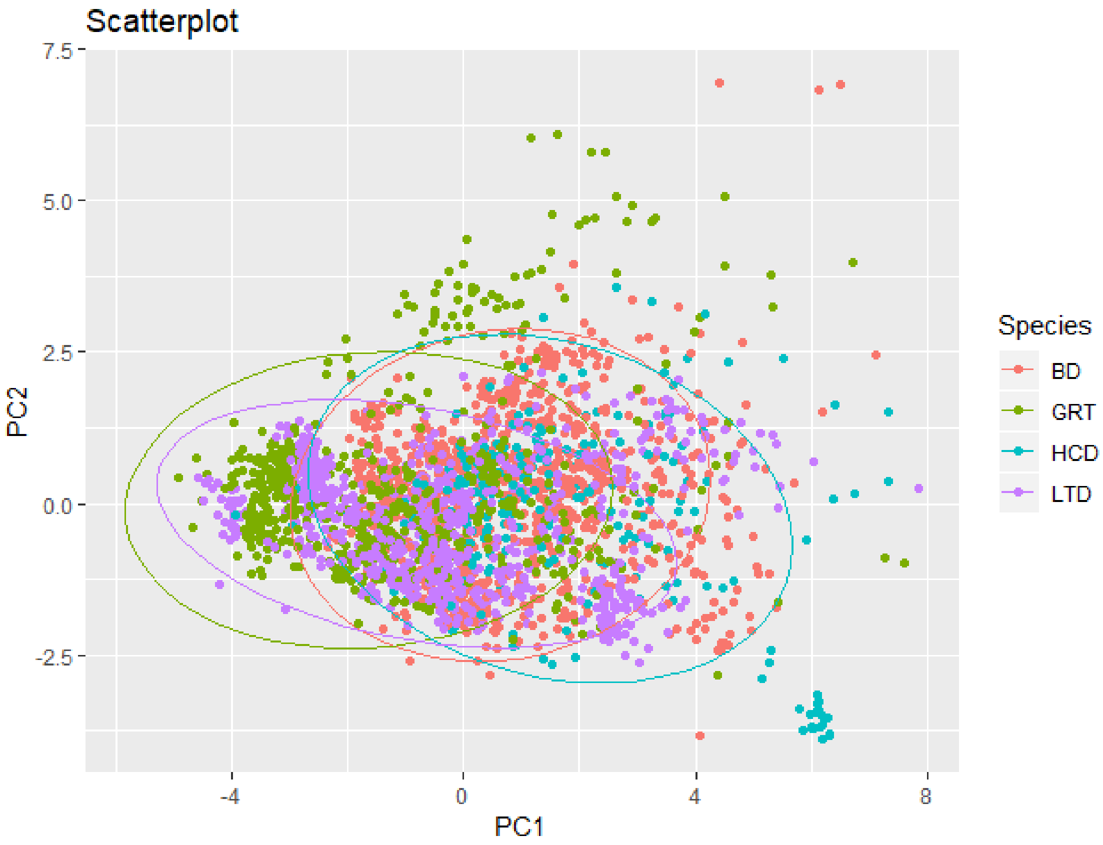

Figure 6-8 Plot of PC scores for PC1 vs PC2 for species-specific note types.

I plotted each individual variable against species (Figure *6-9* to Figure *6-13*) to understand their distribution patterns between different species. There was significant difference of the mean of different acoustic traits amongst all the species as drongos as a group, as well as pair-wise difference between most species of drongos for every parameter *Table 6-7*.

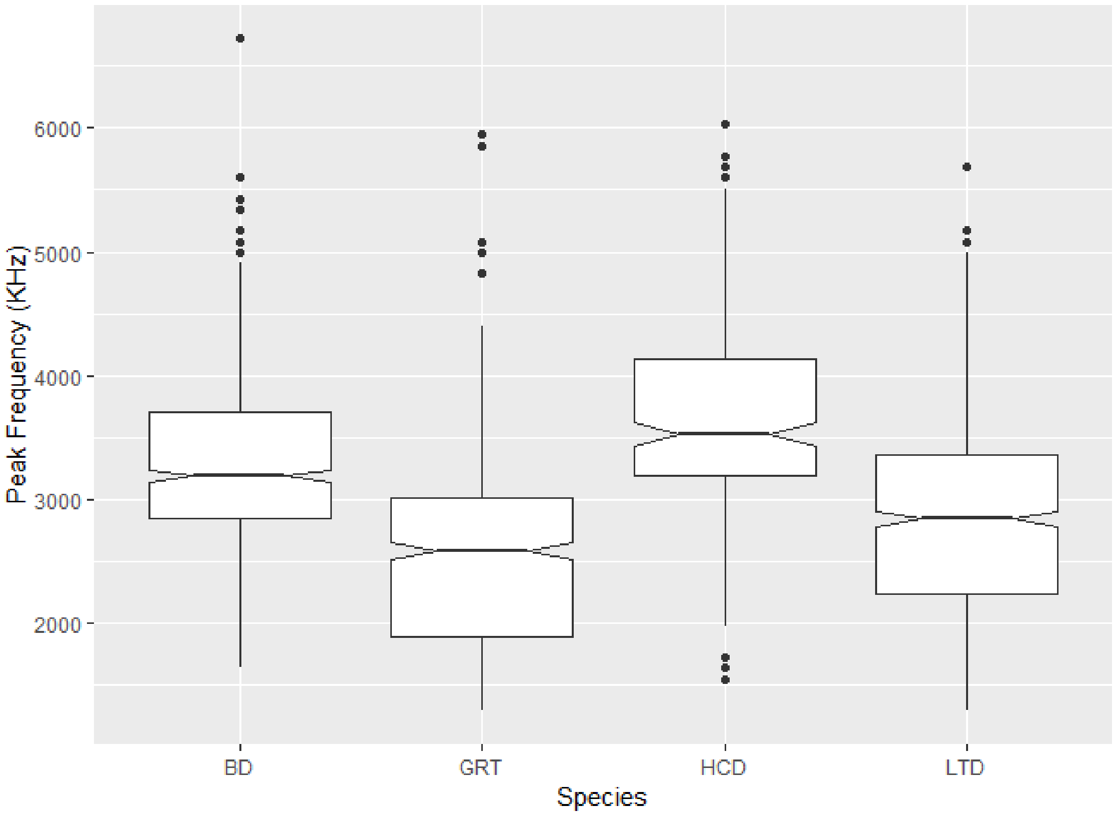

Figure 6-9 Peak frequency across different drongo species. Note: HCD- Hair-crested Drongo; BD- Bronzed Drongo; GRT- Greater Racket-tailed Drongo; LTD- Lesser Racket-tailed Drongo.

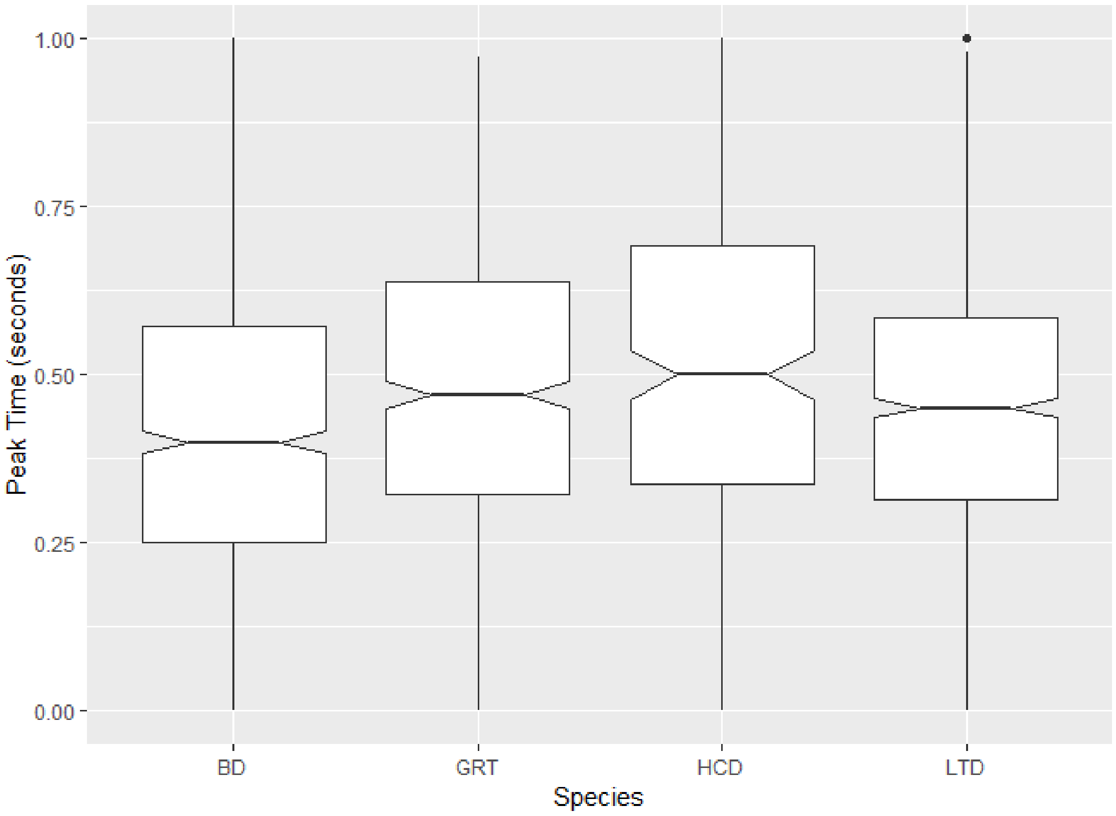

Figure 6-10 Peak time across the four drongos. Note: HCD- Hair-crested Drongo; BD- Bronzed Drongo; GRT- Greater Racket-tailed Drongo; LTD- Lesser Racket-tailed Drongo.

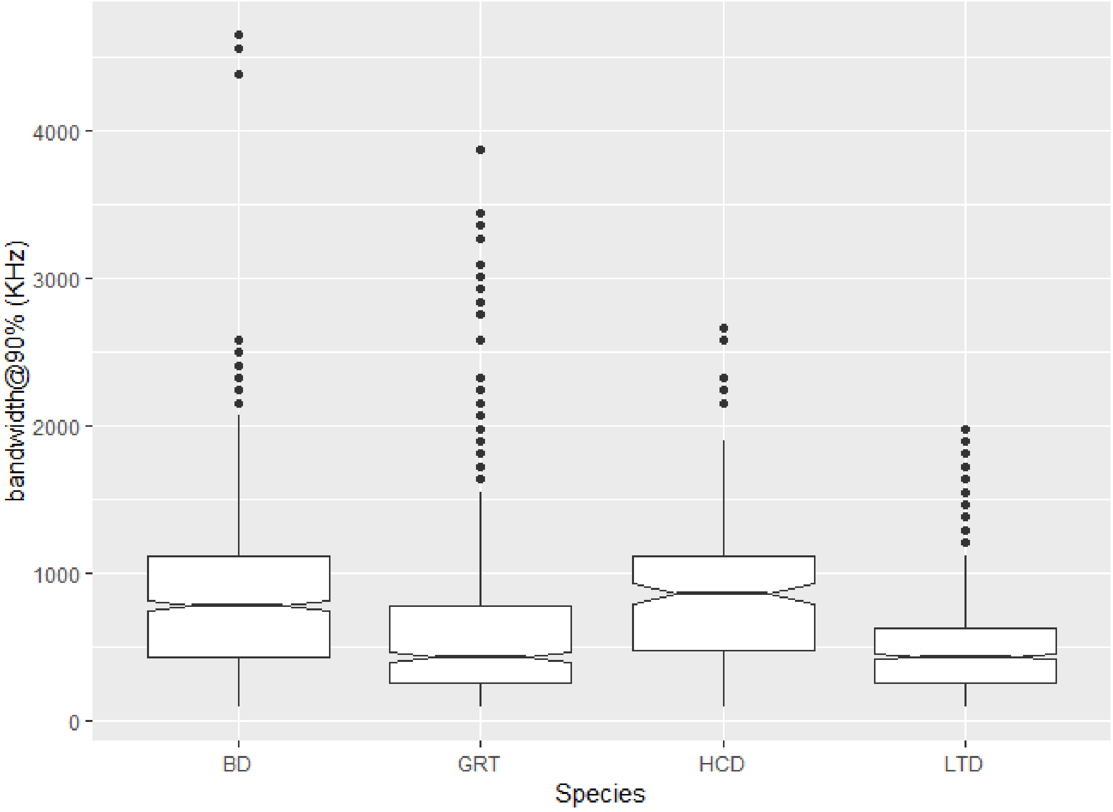

Figure 6-11 Bandwidth @90% across the drongo species). Note: HCD- Hair-crested Drongo; BD- Bronzed Drongo; GRT- Greater Racket-tailed Drongo; LTD- Lesser Racket-tailed Drongo.

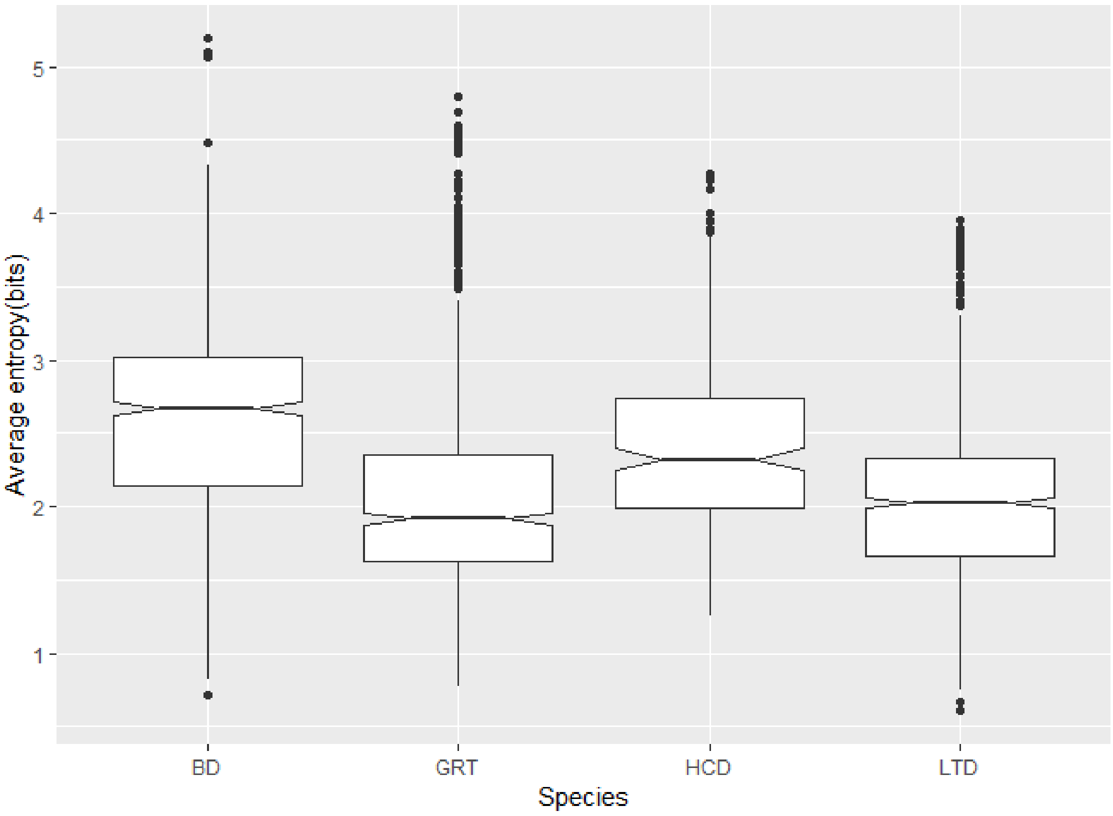

Figure 6-12 Average entropy across four drongo species. Note: HCD- Hair-crested Drongo; BD- Bronzed Drongo; GRT- Greater Racket-tailed Drongo; LTD- Lesser Racket-tailed Drongo.

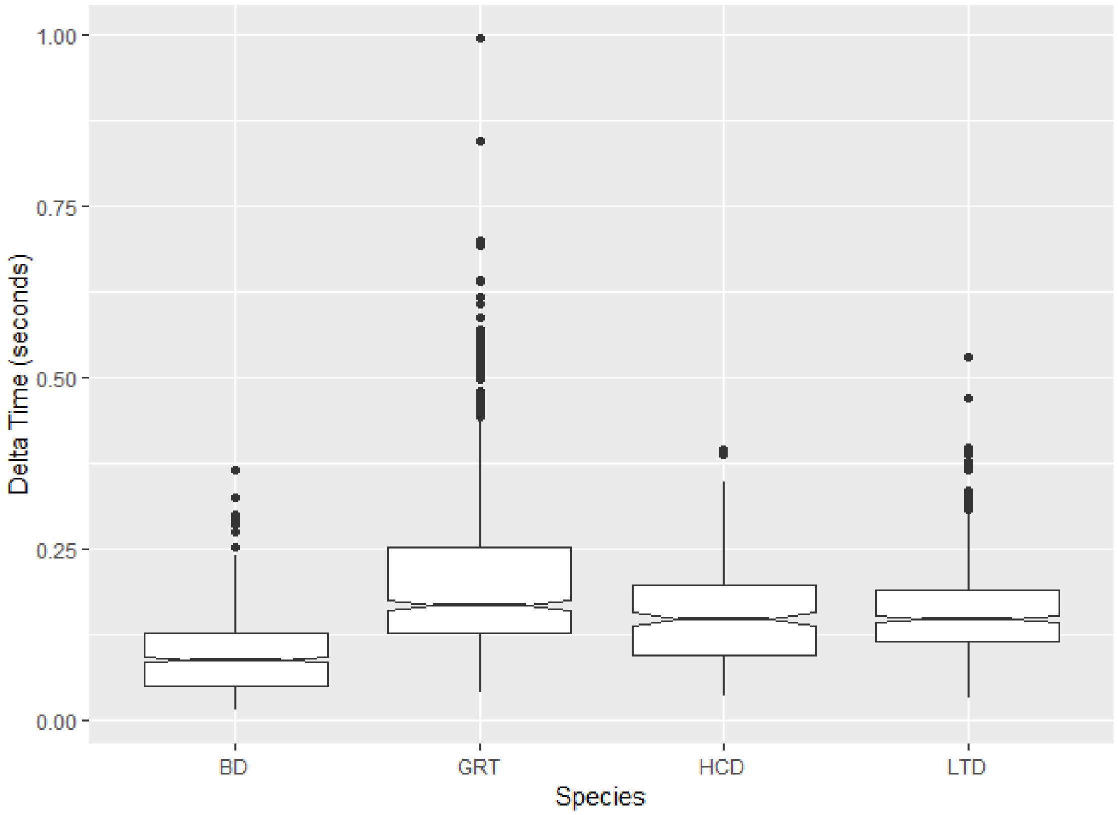

Figure 6-13 Delta time across four drongo species. Note: HCD- Hair-crested Drongo; BD- Bronzed Drongo; GRT- Greater Racket-tailed Drongo; LTD- Lesser Racket-tailed Drongo.

Table 6-7 Comparison of acoustic traits across species

Variable	**ANOVA F-value**	**p-value**
Peak Frequency	195.4	2e-16
Bandwidth @ 90%	68.44	2e-16
Average Entropy	101.6	2e-16
Delta time	256	2e-16
Peak time relative	21.76	6.44E-14

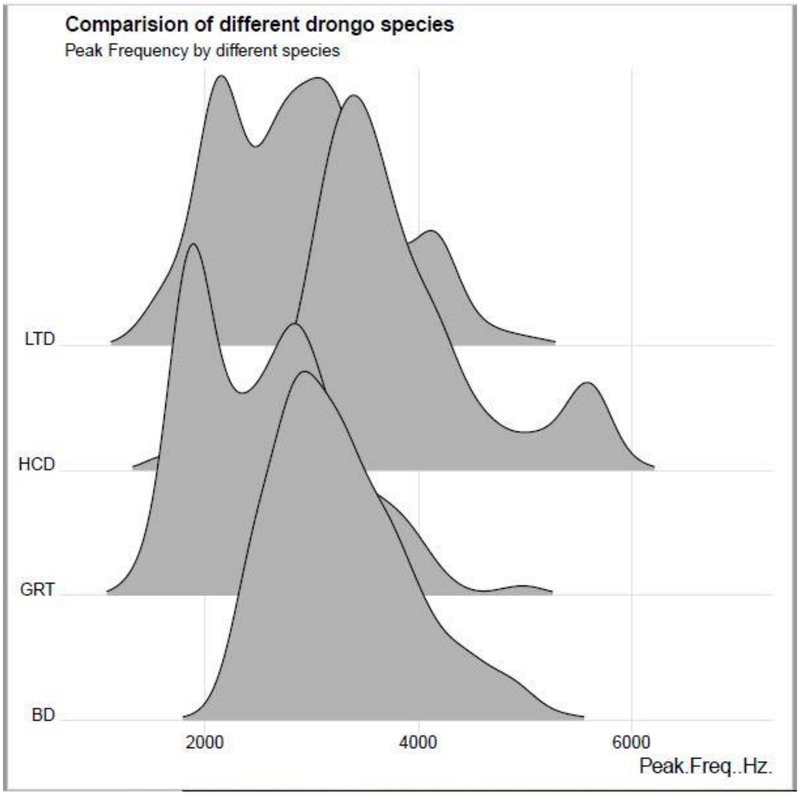

Figure 6-14Density plot of peak frequency

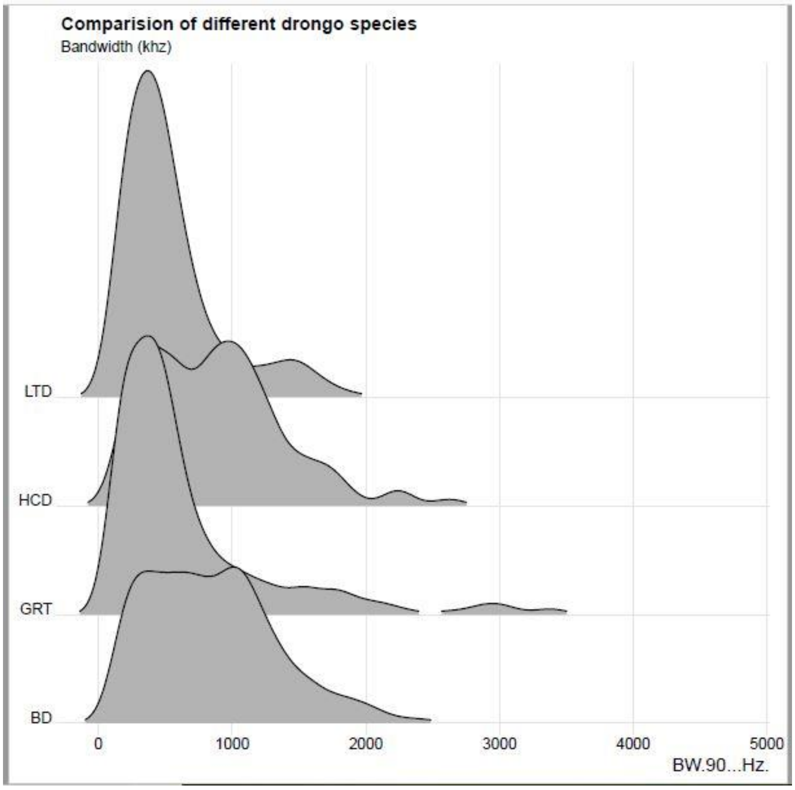

Figure 6-15Density plot of Bandwidth

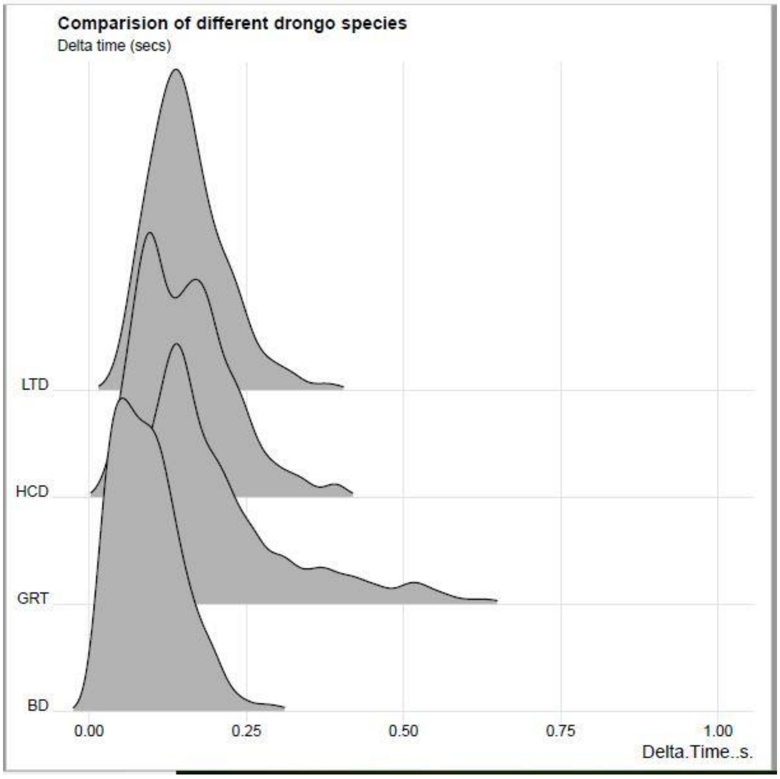

Figure 6-16Density plot of delta time

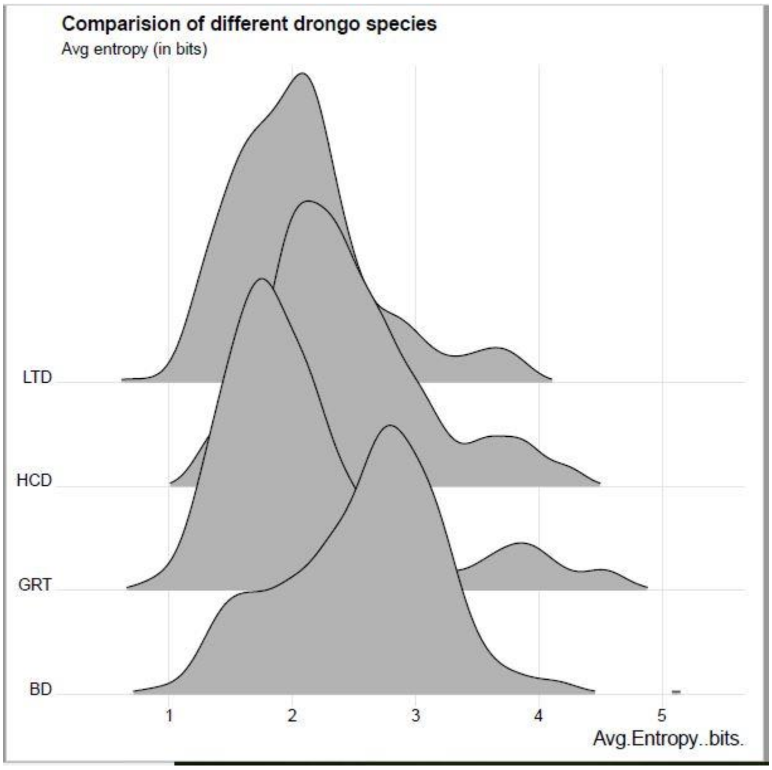

Figure 6-17density plot of average entropy

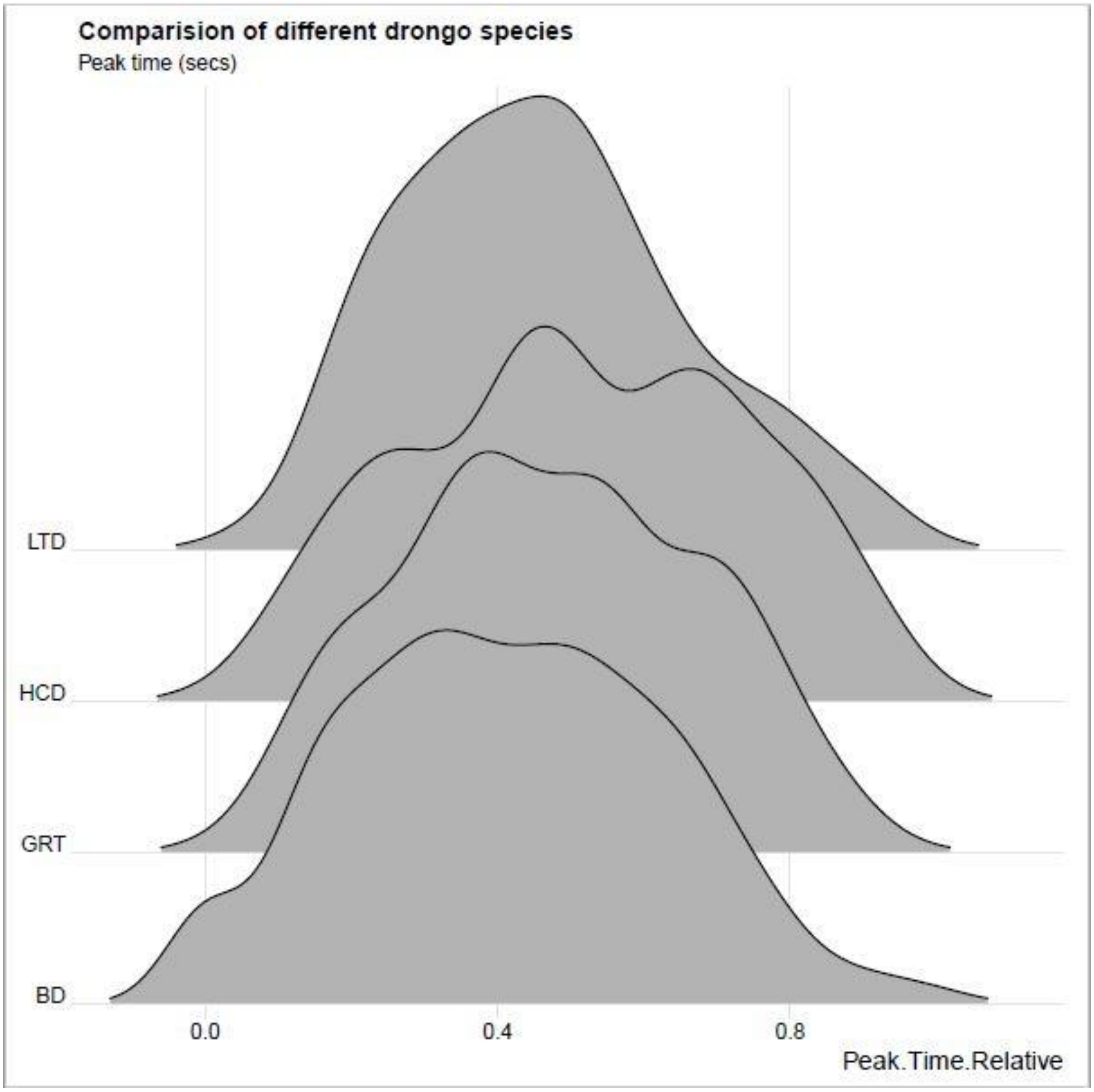

Figure 6-18Density plot of peak time relative

The distributions of the acoustic traits were significantly different for each drongo species pair.

Because of variability in parameter value distributions in each species, and as it was not possible to record the context of calling for each instance, I explored the parameter range most frequently used by each species, i.e. from the 25-75 quartile range. I did an ANOVA followed by a Tukey's HSD test for this dataset, summarised in *Table 6-8*.

Table 6-8 - Results of ANOVA between species for the dataset containing only the most frequently used information, i.e. from 25-75th quantile.

Variable	**ANOVA F-value**	**p-value**
Peak Frequency	548.2	2e-16
BW	501.4	2e-16
Entropy	950.5	2e-16
Delta time	783	2e-16
Peak time relative	74.59	6.44E-14

6.4 Vocal activity pattern

A total of 60 hours of AudioMoth data was analysed. I only analysed the data set from 04:00 to 18:00, i.e. from one hour before sunrise to one hour after sunset. The vocal activity of each drongo was plotted as the number of detections of vocalizations heard in each hour vs time. They were visualised as circular plots. The Bronzed Drongo had two vocal activity peaks- one from 0700hrs to 1000hrs, and the other from 1300hrs to 1700hrs. The Greater Racket-tailed Drongo also had two noticeable peaks in vocal activity, one from 0730hrs to 0930hrs and the other from 1500hrs to 1600hrs. It also had smaller peaks in early mornings (0400-0500hr) as well as late evening (1700-1800hr). The Lesser Racket-tailed Drongo had only one prominent vocal activity peak, i.e. from 0700hr to 0900hr **Error! Reference source not found.**

To calculate the overlap between the activity patterns of two species, I used the package 'overlap'. The coefficient of overlap is given in *Table 6-9*

Table 6-9 Coefficient of overlap in vocal activity between drongo species pairs.

Species pair	**coefficient of overlapping after bootstrap**
Bronzed Drongo-Hair-crested Drongo	0.6
Bronzed Drongo-Greater Racket-tailed Drongo	0.79
Bronzed Drongo-Lesser Racket-tailed Drongo	0.762
Lesser Racket-tailed Drongo-Hair-crested Drongo	0.71
Hair-crested Drongo-Greater Racket-tailed Drongo	0.57
Lesser Racket-tailed Drongo-Greater Racket-tailed Drongo	0.72

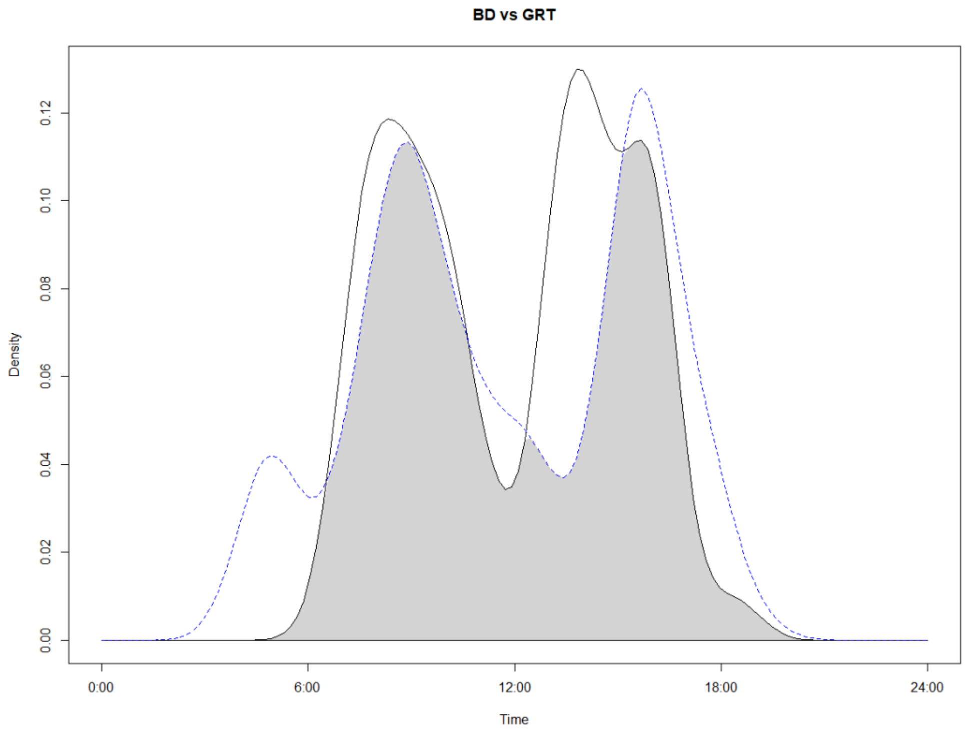

Figure 6-19Temporal overlap between Bronzed and Greter Racket-tailed Drongo

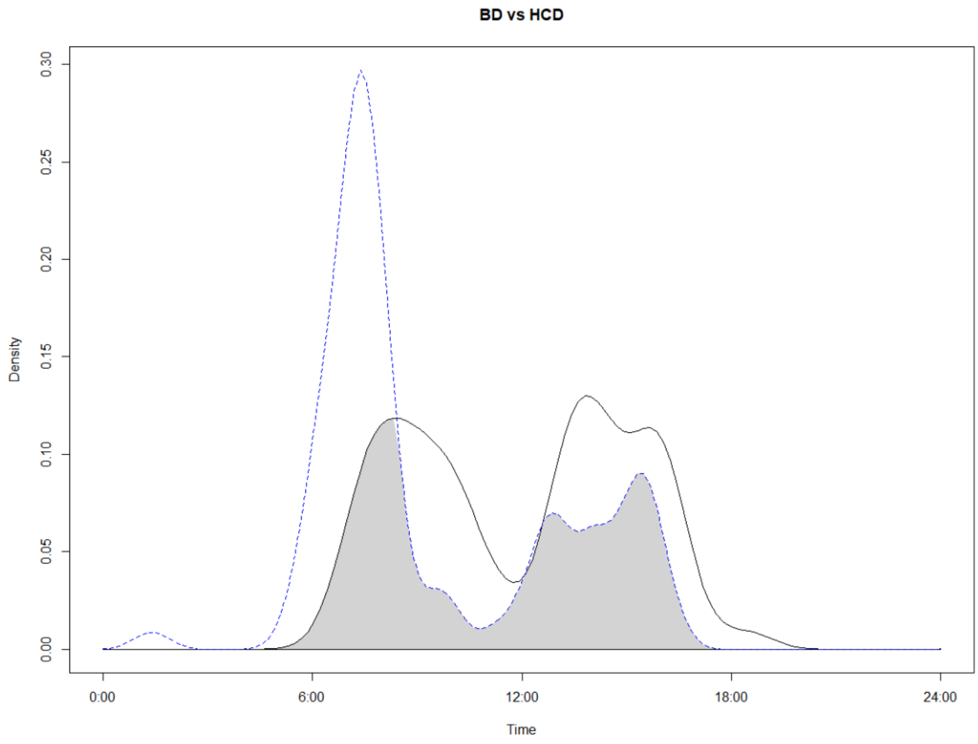

Figure 6-20Temporal overlap between Bronzed and Hair-crested Drongo

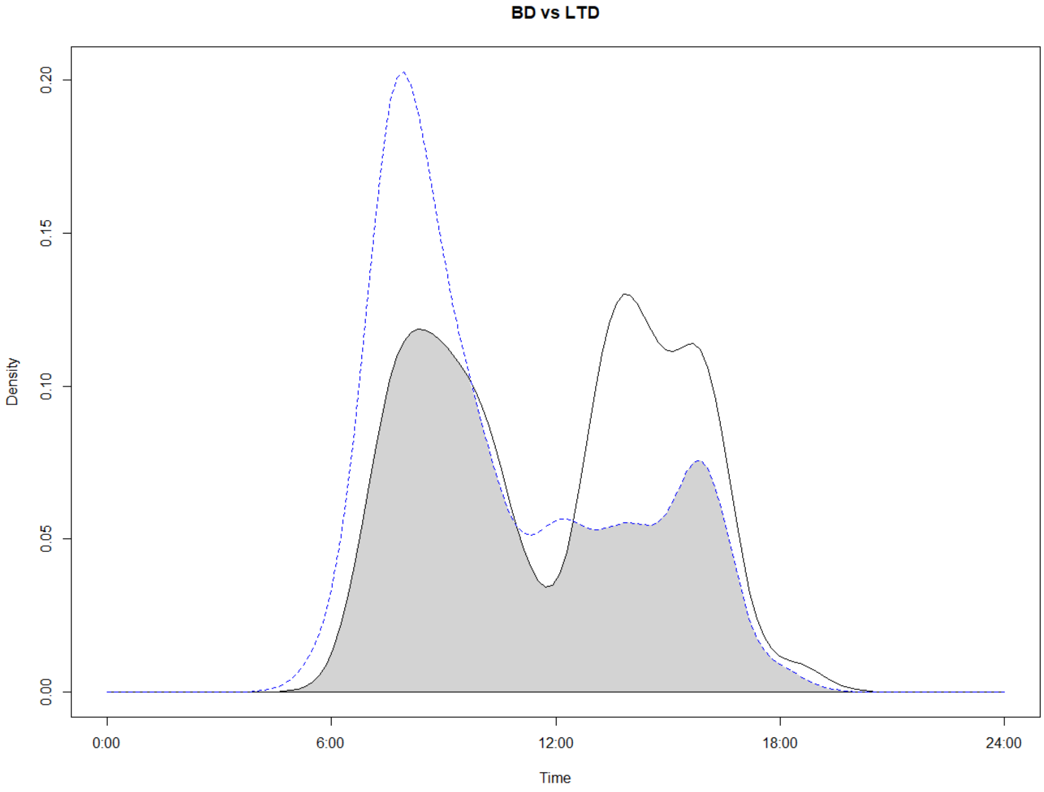

Figure 6-21Temporal overlap between Bronzed and Lesser Racket-tailed Drongo

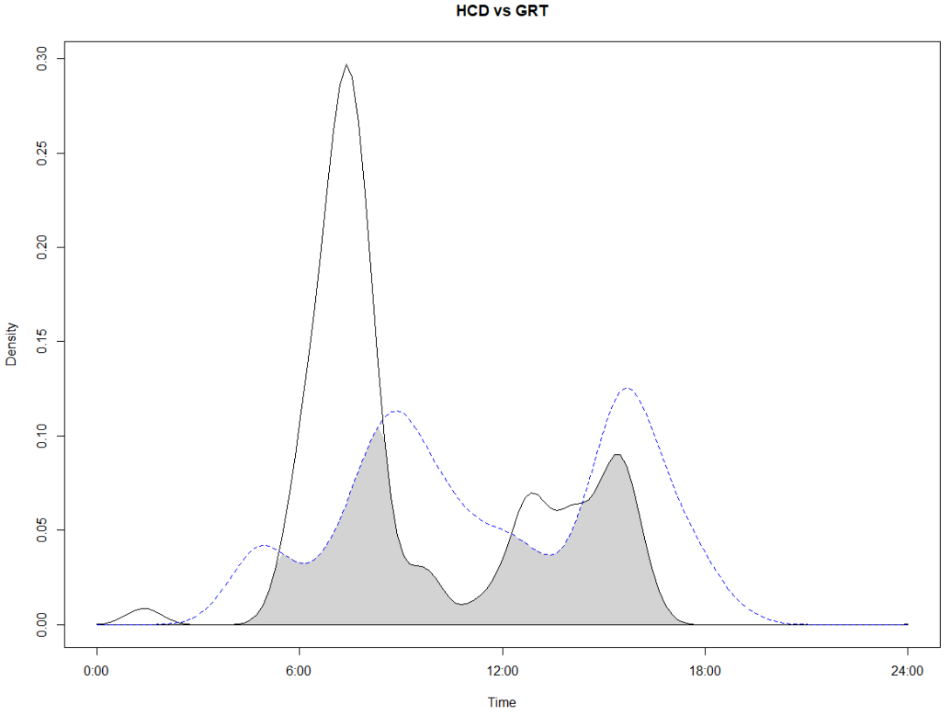

Figure 6-22Temporal overlap between Hair-crested and Greater Racket-tailed Drongo

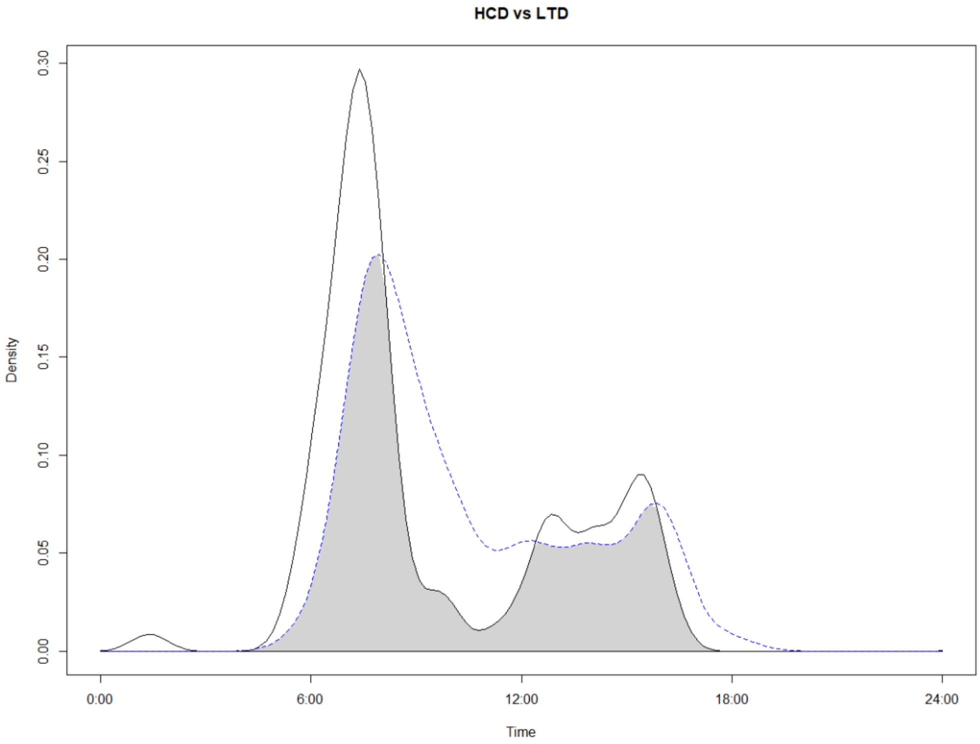

Figure 6-23Temporal overlap between Hair-crested and Lesser Racket-tailed Drongo

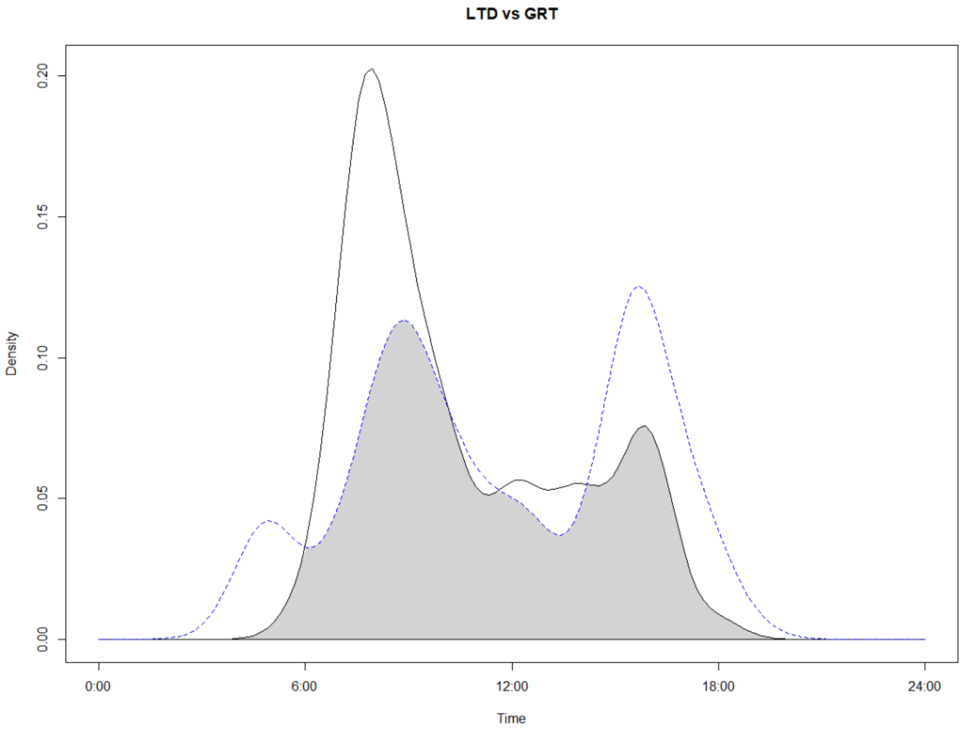

Figure 6-24Temporal overlap between Lesser and Greater Racket-tailed Drongo

6.5 Perch heights

Song perch heights of all four species of drongos showed significant difference (F=87.27, p=2.2e-16). The Hair-crested Drongo (n=46) occupied the highest perch (31.5±2.6m), followed by Bronzed Drongo(n=100) (24±7.27m). The Lesser Racket-tailed Drongo (n=48) (13±5.9m) and the Greater Racket-tailed Drongo(n=20) (12.42±6.8 m) occupied the same median heights *Figure 6-25*.

Significant differences were found in all pairs of species, except for Lesser Rack et-tailed Drongo and Greater Racket-tailed Drongo (p=0.9853). This shows highl y significant difference in perch heights across the species.

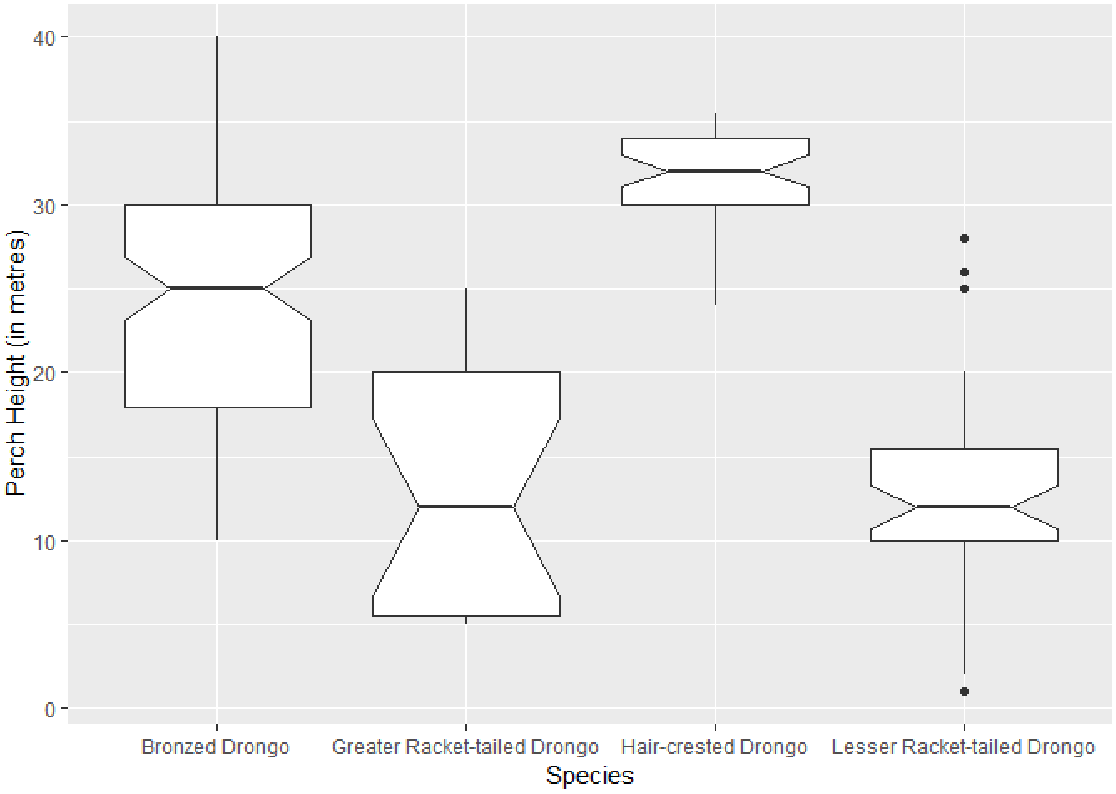

Figure 6-25 Perch heights used by Bronzed drongo, Greater Racket-tailed Drongo, Hair-crested Drongo and Lesser Racket-tailed Drongo

7 DISCUSSION

Competitive exclusion states that ecologically similar species will either outcompete each other or develop divergent traits to coexist. Environment filtering, however, says how species which are similar in their ecological traits co-exist in sympatry by virtue of the environment being a selection force (Kraft et al. 2014). Character displacement, or the difference in any trait characteristic among species present in sympatry, and the loss of it in entirety or in parts, where they do not overlap in range has been suggestive as a way by which closely related species can co-exist (Wilson and Brown 1955; Grant 1972).

Acoustic traits are highly important for several taxa of organisms, ranging from insects, fishes to birds and mammals. It is an especially important trait for species which live in habitats where visual and olfactory traits fail to be effective, e.g. In dense forests, oceans (Bradbury and Vehrencamp 1998). Acoustic traits are of particular importance to birds which use vocalization for several functions like mate selection, territorial defence, kleptoparasitism, species identification, etc (Seddon 2005; Catchpole and Slater 2003, Flower et al. 2014). Acoustic traits, however, are subject to several changes and distortions imposed by the habitat as well as other species present in vicinity (Luther 2009; Brumm and Slabbekoorn 2005). Species which are closely related are more susceptible to masking interference because of they are related and thus have similar traits- phylogenetic signal in traits – and thus their shared ancestry influence their biological capability of vocalization. (Blomberg and Garland 2002).

In this study, we looked into a group of passerine birds, the drongos- a group of related but sympatric birds, and how they separate out their niche to co-exist. We also looked into the ecological strategies that drongos use to prevent masking interference from congeners.

Density estimation

The Bronzed Drongo was the most abundant drongo in the study area (37.53±7.54/km^2). The Hair-crested Drongo, Greater and the Lesser Racket-tailed Drongo are present in comparable densities-5.73±3.52/km^2, 7.03±2.33/km^2 and 10.24±1.98/km^2, respectively. Densities of species, especially closely related species, is important as it dictates spatial segregation as well as competition for resources, including the acoustic space. Species in equal densities are more likely to compete with each other than species with varying densities. For example, the Hair-crested Drongo is a nectarivore and migrates locally with the blooming of flowers like *Bombax*. Apart from this, it does not use vocalization for as many functions as the other drongo species. Thus, its low density and limited amount of function for its vocalization can likely not compete for an acoustic space with the other drongo species. However, it is interesting to note that the Greater Racket-tailed Drongo and the Lesser Racket-tailed Drongo occurs in similar densities in the study area. This pair of species overlaps in the multidimensional acoustic space and also occupies similar heights.

Phylogenetic signal in acoustic traits

Analysis of phylogenetic signal produced less phylogenetic signal than is expected under Brownian motion. This means that the patterns in the acoustic traits observed are not a by-product of shared ancestry, but rather due to other selective pressures acting on the trait. Therefore, it can be ruled out that any similarity in acoustic traits is a result of shared ancestry.

Acoustic trait patterns in drongos

For acoustically communicating species, the acoustic channel can be regarded as an acoustic resource (Schmidt and Balakrishnan 2014), and with large number of vocal species, especially closely related members, the problem of masking interference increases. Thus, a species is expected to partition in a multidimensional space, including spectral and temporal properties.

The study shows evidence of overlap in the multidimensional acoustic space between the four species of drongo (*Figure 6-8*). However, when the acoustic parameters were analysed in their most frequently used ranges, there was significant difference between species pairs in most of the acoustic parameters used (except for no significant difference in delta time between Lesser Racket-tailed Drongo and Hair-crested Drongo).

Owing to the plasticity of their vocalization and in particular, their capability of mimicking other species (Ali 1943; Grimmett et al. 2013), drongos have a high diversity of notes in their repertoire, unlike species which do not learn their calls like suboscines. The acoustic space can be thought of as part of the fundamental niche of a species occupies. Overlaps in the acoustic space are suggestive of the breadth of auditory capabilities the species is able to extend its niche to, but might not be functionally able to perform at its peak at the ends/edges of these ranges either in spectral or temporal domains. It is also interesting to note that mimicry increases the fundamental acoustic space for the drongos, which is most noticeable in the Greater Racket-tailed Drongo (will add Reference to figure). Mimicry in Greater Racket-tailed Drongo has been documented to serve several social and highly contextual functions like attracting mix-flocks (Goodale 2006b), alarm calling, mobbing (Goodale 2006), kleptoparasitism (Satischandra 2010) in addition to mate attraction and territorial defence. Attracting a mix flock is of particular importance for a drongo, as it increases foraging efficiency (S. Satischandra, Kudavidanage, Kotama, & Goodale, 2007). In a study in Sri Lanka, it has been noted that the Greater Racket-tailed Drongo will mimic a variety of species that are usually present in a mix-flock, and couple it with its own species-specific vocalization. This gives the impression of a mix flock being present, and thus deceives the birds to form a flock (Goodale 2006). Although anecdotal, this was seen in case of the Lesser Racket-tailed Drongo as well, which also forms and forages in mix flocks *Figure 7-1* (Round, 2005).

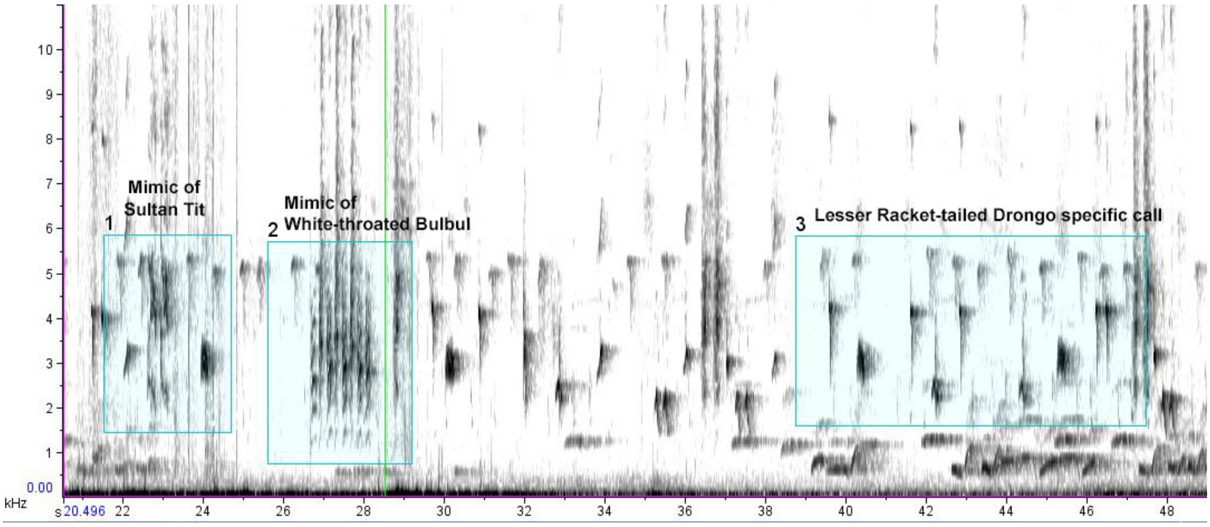

Figure 7-1 Mimicry of Sultan Tit, White-throated Bulbul and species-specific call of the Lesser Racket-tailed Drongo

However, the reason why the species differ significantly when the acoustic parameters are compared individually is that we only consider the range of each variable which is most frequently used by the drongo species, thus excluding any potential effect of outliers and the overall large variability of the species trait. Frequency measures, particularly peak frequency, is an important acoustic parameter for species which communicate acoustically. Higher frequency sounds are more adept at counteracting the masking effect of low frequency noise. This, however, has been demonstrated in urban systems where blackbirds sang at higher frequencies with respect to their conspecifics in wooded habitats. This is an adaptation to counteract the masking by traffic noise (Nemeth et al. 2013)

Perch heights

Song post heights are an important adaptation to counteract the effect of habitat on the acoustic trait of a species and is well documented in insects (Jain and Balakrishnan 2012) and birds (Nemeth et al. 2001; Seddon 2005). Transmission studies have found how greater heights offer better transmission and broadcast area (Ellinger and Hodl 2003; Jain and Balakrishnan 2012). The mid-storey comes as the best suited height for vocalizing animals, because of the dual advantage of lesser foliage density and height above the ground (Schmidt and Balakrishnan 2014). However, very few animals use this stratum because of increased detectability by predators.

The study presents evidence of significant difference in the mean song perch heights between the four species of drongos (*Figure 6-25*). Hair-crested Drongo occupies the highest mean perch height (31.5±2.6m), followed by the Bronzed Drongo (24±7.27m). The Greater Racket-tailed Drongo (12.42±6.8 m) and the Lesser Racket-tailed Drongo(13±5.9m), however, have no significant difference in their mean song perch heights. Similar patterns of vertical stratification have been seen in drongos in an evergreen and moist deciduous forest of Thekkady in Kerala (Vijayan 1984), where the Bronzed Drongo occupied the higher strata while the Greater Racket-tailed Drongo occupied the lower strata. However, it was also recorded in the same study, that in lower camp where the habitat is primarily dry deciduous, the Bronzed Drongo occupied the lower strata while the Greater Racket-tailed Drongo occupied the higher strata.

One reason for the Greater and Lesser Racket-tailed Drongo to occupy similar song post height is that they are phylogenetically much more closely related to one another than to other drongo species in the study area ((Pasquet & Cruaud, 2007)). Additionally, they are also similar in their morphology (Ali 1943) which might explain their preference for a similar perch height. Although the two species did not have significant difference in peak frequency and average entropy when the entire range of note diversity was considered, they did show significant difference in the peak frequencies most frequently used. The song perch height of the Hair-crested Drongo, being the highest, is likely because they are nectarivores (Ali and Ripley 1983) and thus always occupied the higher perches of flowering trees like *Bombax ceiba* and *Erythrina spp*. All the vocal event recorded were when the species was present in either of these trees.

The difference can be a result of its behavioural adaptation to the environment. For example, birds with higher frequency proportionately use higher strata compared to birds with lower frequency. This is because low frequency is more adept at traveling greater distance through dense foliage (Catchpole and Slater

2003). In the four species of drongo, the Hair-crested Drongo, which occupies the highest height (31.5±2.6m) also has the highest peak frequency (3565.3±272.31Hz), while the Greater Racket-tailed Drongo, which occupies the lowest height (12.42±6.8 m) has the lowest peak frequency(2407.3±392.16Hz).

Vocal activity pattern

Species can also partition and thus avoid masking interference from other vocal species by calling at different times (Schmidt & Balakrishnan, 2014). There is evidence of this from several species of birds (Cody and Brown 1969; Ficken et al. 1974; Wasserman 1977; Smith and Norman 1979).

In this study, we tested the hypothesis that different species of drongos will call at different times of the day to avoid masking one another. Passive acoustic recording in the study area throughout the day revealed different vocal activities in the four species of drongo- The Bronzed Drongo had two vocal activity peaks- one from 0700hrs to 1000hrs, and the other from 1300hrs to 1700hrs. The Greater Racket-tailed Drongo also had two noticeable peaks in vocal activity, one from 0730hrs to 0930hrs and the other from 1500hrs to 1600hrs. It also had smaller peaks in early mornings (0400-0500hr) as well as late evening (1700-1800hr). The Lesser Racket-tailed Drongo had only one prominent vocal activity peak, i.e. from 0700hr to 0900hr. However, there is significant overlap in between the activity patterns of the drongos. Thus, drongos do not seem to segregate in vocal activity pattern. This is, however, not surprising, because the vocal activity peaks for each drongo corresponds to peak bird activity period in the forest (Robbins 1981) and being insectivores, the three species of drongo, viz. Bronzed Drongo, Lesser Racket-tailed Drongo and Greater Racket-tailed Drongo must optimise foraging and using vocalization in specific context during these activity windows.

Table 7-1 Summary of traits compared pair-wise between each species of drongo. Note: HCD- Hair-crested Drongo;BD- Bronzed Drongo; GRT- Greater Racket-tailed Drongo; LTD- Lesser Racket-tailed Drongo. ‘Yes’ -significant difference, ‘No’ is similar or no difference.

Species pair	Perch height	temporal activity	Peak Frequency	Peak Time	Entropy	Bandwidth @ 90%	delta time	Food habits
BD-LTD	Yes	No	Yes	Yes	Yes	Yes	Yes	Both Insectivores
BD-GRT	Yes	No	Yes	Yes	Yes	Yes	Yes	Both Insectivores
BD-HCD	Yes	No	Yes	Yes	Yes	Yes	Yes	HCD nectarivore
LTD-GRT	No	No	Yes	Yes	Yes	Yes	Yes	Both Insectivores
LTD-HCD	Yes	No	Yes	Yes	Yes	Yes	No	HCD nectarivore
GRT-HCD	Yes	No	Yes	Yes	Yes	Yes	Yes	HCD nectarivore

8 CONCLUSION

The study presents evidence of multiple ways by which drongos ensure they partition themselves in order to avoid masking interference from closely related congeners. The Bronzed Drongo is the most abundant drongo species in the study area, while the Hair-crested Drongo, Lesser Racket-tailed Drongo and Greater Racket-tailed Drongo occur in similar abundance in the study area. Analysis of phylogenetic signal reveals low signal in the acoustic traits, which mean the patterns in acoustic traits are not as a result of shared ancestry.

Although the fundamental acoustic niche breadth of each species of drongo is large and is overlapping with one another as a result of the species capability to produce diverse vocal repertoire, the species differ in their individual acoustic parameters in the spectral and temporal domain. We present evidence of difference in the overall acoustic parameters between species when we consider the most frequently used range of acoustic parameter.

The study also elucidates significant difference in perch heights across species, expect for between the Greater and the Lesser Racket-tailed Drongo, which occupy similar heights. The four species of drongo also do not show difference in their vocal activity pattern, with overlapping activities throughout the day.

Although many studies on acoustic partitioning have been done on birds which do not learn their vocalization, passerines, owing to their vocal flexibility offer an interesting study group as they have an expanded range of behavioural and ecological adaptations to ensure they are not masked in their acoustic space. Studies on drongos, especially on the mimicry of the other species of drongo, will give valuable insights into the role of mimicry in these hitherto unexplored species. Furthermore, rigorous study on vocal activity pattern on a larger scale, as well as acoustic transmission studies can be done to gain newer insights into the acoustic traits of drongos.

9 REFERENCES

Bee, M. A., & Micheyl, C. (2008). The Cocktail Party Problem: What Is It? How Can It Be Solved? And Why Should Animal Behaviorists Study It? *Journal of Comparative Psychology*, *122*(3), 235–251. doi: 10.1037/0735-7036.122.3.235

Flower, T. (2011). Fork-tailed drongos use deceptive mimicked alarm calls to steal food. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1711), 1548–1555. doi: 10.1098/rspb.2010.1932

Flower, T. P., Gribble, M., & Ridley, A. R. (2014). Deception by Flexible Alarm Mimicry. *Science*, *344*(2 May 2014), 513–516.

Goodale, E., & Kotagama, S. W. (2006). Alarm Calling in Sri Lankan Mixed-Species Bird Flocks. *The Auk*, *122*(1), 108. doi: 10.1642/0004-8038(2005)122[0108:acislm]2.0.co;2

Grant, P. R. (1972). *Convergent and divergent character displacement*. (March), 39–68.

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*(5), 592–599. doi: 10.1111/1365-2435.12345

Krishnan, A., & Tamma, K. (2016). *Divergent morphological and acoustic traits in sympatric communities of Asian barbets Subject Category : Subject Areas :*

Pasquet, E., & Cruaud, C. (2007). *Evolutionary history and biogeography of the drongos (Dicruridae), a tropical Old World clade of corvoid passerines*. *45*, 158–167. doi: 10.1016/j.ympev.2007.03.010

Popp, J. W., Ficken, R. W., & Reinartz, J. A. (2018). *Short-Term Temporal Avoidance of Interspecific Acoustic Interference among Forest Birds Author (s): James W . Popp , Robert W . Ficken and James A . Reinartz Published by : American Ornithological Society Stable URL : https://www.jstor.org/stable/408671*. *102*(4), 744–748.

Round, P. D. (2005). Foragin of Greater Racket-tailed Drongo and Lesser Racket-tailed Drongo in Mixed-species Bird Flocks at Khao Yai National Park. *Nat. Hist. Bull. Siam Soc.*, *52*(1), 115–117.

Satischandra, S. H. K., Kodituwakku, P., Kotagama, S. W., & Goodale, E. (2010). Assessing “false” alarm calls by a drongo (Dicrurus paradiseus) in mixed-species bird flocks. *Behavioral Ecology*, *21*(2), 396–403. doi: 10.1093/beheco/arp203

Satischandra, S., Kudavidanage, E., Kotama, S., & Goodale, E. (2007). The benefits of joining mixed-species flocks for greater racket-tailed drongos Dicrurus paradiseus. *Forktail*, *23*, 145–148. Retrieved from http://birdingasia.org/wp-content/uploads/2012/09/Satischandra-Drongos.pdf

Schmidt, A. K. D., & Balakrishnan, R. (2014). *Ecology of acoustic signalling and the problem of masking interference in insects*. doi: 10.1007/s00359-014-0955-6

Popp, J.W., 1989. Temporal aspects of singing interactions among territorial ovenbirds (Seiurus aurocapillus). *Ethology*, *82*(2), pp.127-133.

Nemeth, E., Pieretti, N., Zollinger, S.A., Geberzahn, N., Partecke, J., Miranda, A.C. and Brumm, H., 2013. Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1754), p.20122798.

Cody, M.L. and Brown, J.H., 1969. Song asynchrony in neighbouring bird species. *Nature*, *222*(5195), p.778.

Planque, R. and Slabbekoorn, H., 2008. Spectral overlap in songs and temporal avoidance in a Peruvian bird assemblage. *Ethology*, *114*(3), pp.262-271.

Smith, D.G. and Norman, D.O., 1979. " Leader-Follower" Singing in Red-Winged Blackbirds. *The Condor*, *81*(1), pp.83-84.

Blomberg, S.P. and Garland Jr, T., 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology*, *15*(6), pp.899-910.

Blomberg, S.P., Garland, T. and Ives, A.R., 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, *57*(4), pp.717-745.

Pagel, M., 1999. Inferring the historical patterns of biological evolution. *Nature*, *401*(6756), p.877.

Cavender-Bares, J., Kozak, K.H., Fine, P.V. and Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. *Ecology letters*, *12*(7), pp.693-715.

Cavender-Bares, J., Ackerly, D.D., Baum, D.A. and Bazzaz, F.A., 2004. Phylogenetic overdispersion in Floridian oak communities. *The American Naturalist*, *163*(6), pp.823-843.

Catchpole, C.K. and Slater, P.J., 2003. *Bird song: biological themes and variations*. Cambridge university press.

Marler, P.R. and Slabbekoorn, H., 2004. *Nature's music: the science of birdsong*. Elsevier.

Grimmett, R., Inskipp, C. and Inskipp, T., 2013. *Birds of the Indian Subcontinent: India, Pakistan, Sri Lanka, Nepal, Bhutan, Bangladesh and the Maldives*. Bloomsbury Publishing.

Ali, S. and Ripley, S.D., 1980. *Handbook of the birds of India and Pakistan, together with those of Bangladesh, Nepal, Bhutan, and Sri Lanka*. Oxford University Press.

Ali, S., 1943. *The book of Indian birds*. The Bombay Natural History Society; Bombay.

Crawley, M.J., 2012. *The R book*. John Wiley & Sons.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3 217-223.

Pasquet, E., Pons, J.M., Fuchs, J., Cruaud, C. and Bretagnolle, V., 2007. Evolutionary history and biogeography of the drongos (Dicruridae), a tropical Old World clade of corvoid passerines. *Molecular phylogenetics and evolution*, *45*(1), pp.158-167.

Kakati, K., Raghavan, R., Chellam, R., Qureshi, Q. and Chivers, D.J., 2009. Status of Western Hoolock Gibbon (Hoolock hoolock) populations in fragmented forests of eastern Assam. *Primate Conservation*, *24*(1), pp.127-138.

Hultsch, H. and Todt, D., 1982. Temporal performance roles during vocal interactions in nightingales (Luscinia megarhynchos B.). *Behavioral Ecology and Sociobiology*, *11*(4), pp.253-260.