1 **"Acoustic space overlap in sympatric drongos (Aves: Dicruridae) and spatial segregation in**
2 **a South Asian tropical rainforest"**
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12 **Abstract:** A diverse array of animals use a multidimensional acoustic space as a primary source
13 of communication, especially in habitats where other signals are limited. However, in complex
14 habitats, species must contend with other co-occurring species to send their message in a backdrop
15 of ambient noise. This is exacerbated in closely related species that occur in sympatry, and we do
16 not know how species that learn their vocalization and have diverse repertoires partition their
17 acoustic space. In this study, we studied four species of closely related group of birds, the drongos,
18 in a tropical evergreen forest in South Asia. We made field vocal recordings as well as estimated
19 song perch heights in the four species from December 2018-April 2019. Using ordination methods
20 like PCA and LDA, we find wide overlap in the acoustic space in the four sympatric drongos. We,
21 however, find that drongos segregate vertically. We hypothesize that drongos overlap in acoustic
22 space owing to their ability to mimic other species, which increases their acoustic signal breadth.
23 To partition their acoustic space, drongos potentially vocalize from different perch heights. Our
24 study broadens our understanding of how a vocally diverse group of birds may partition in the
25 acoustic signal space.
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27 **Keywords:** mimicry, signal space, tropical forest, bioacoustics, passerines, acoustics
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Introduction

How closely related species, occurring in sympatry, successfully partition resource use is an active area of research in ecology. Acoustic signal space- a multidimensional space described by the spectral and temporal features of acoustic signals (Chhaya et al. 2021)- is a resource that is particularly important for species that vocalize for a wide variety of functions. These functions include mate attraction, territory defense, social cohesion in cooperative behavior or mixed foraging (Nelson & Marler 1990; Bradbury & Vehrencamp 1998). However, as more species co-occur in multispecies communities, individual species must devise strategies to efficiently communicate in a 'cocktail' of background noise (Bee & Micheyl 2008). For example, birds in tropical forests vocalized at lower frequency or completely stopped vocalizing when a single cicada species was vocalizing at the same time and frequency (Kirschel et al. 2009; Hart et al. 2015).

The problem of avoiding masking interference is further amplified for closely related sympatric species that need to devise diverse strategies to avoid masking (Schmidt & Balakrishnan 2015). To ensure unambiguous species recognition and prevent hybridization between species, songs of closely related sympatric species need to be more divergent (The species recognition hypothesis, Seddon 2005). Birds are no exception. Birds use vocalization for a wide range of functions, including territory defense, mate attraction, resource defense (Catchpole & Slater 2003) as well as other social functions like kleptoparasitism, associating with heterospecific flocks, and raising alarm against predators (Marler & Slabbekoorn 2004; Goodale & Kotagama 2006). In birds that occur in sympatry, many studies have shown patterns of spectral divergence. For example, in a large group of South American antbirds (Thamnophilidae), there is evidence for greater song divergence in closely related, sympatric species than in allopatric species (Seddon 2005). Similar examples abound from several bird groups (barbets, Krishnan & Tamma 2016; Wren-warblers, Chitnis et al. 2020; Asian Cuckoos, Mei et al. 2023). However, these studies have been done on species who do not exhibit plasticity in their vocalization. Many passerine birds, 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 behavioral and physics-based strategies they may employ to "get the message across" in an acoustically crowded environment. This is further important in complex and dense habitats like forests, where acoustic traits are more important because other traits like visual cues are not as effective owing to dense vegetation and limited visibility (Catchpole & Slater 2003). Moreover, while there is support for signal divergence and partitioning, many sympatric groups of birds also exhibit overlap in signal space(De Kort et al. 2002; Haavie et al. 2004; Madabhushi 2023) suggesting potentially different strategies to avoid masking interference.

Apart from partitioning in acoustic signal space, animals also employ different behavioral strategies to avoid masking interference, especially in complex habitats like tropical evergreen and dry forests as well as open habitats and deserts. For example, there is evidence of different calling perches to potentially avoid interspecific masking (Diwakar & Balakrishnan 2007; Chitnis et al. 2020), temporal partitioning either by calling at different times in spectrally similar species (Planqué & Slabbekoorn 2008; Mohan et al. 2022; Chronister et al. 2023; Kennedy et al. 2023) or finer-scale note-level temporal partitioning. Taken together, these suggest the diverse possibilities employed by animals to avoid masking interference beyond spectral partitioning. However,

93 employing all these strategies together (Difference in spectral, spatial, and temporal properties) is
94 costly and species might employ either strategy to partition in their acoustic signal space. It is thus
95 important to explore the different strategies used by a group of closely related species occurring in
96 sympatry.

97   Here, we study the vocal partitioning in sympatric drongos (Dicruridae) in a lowland
98 evergreen forest in Eastern India. Drongos are a group of highly vocal passerines that are found
99 across Asia, Africa and Australia and comprise 29 species. Drongos occur across varied
100 landscapes, including forests, open habitats, agriculture, and urban spaces. They are known for
101 their vocal diversity by way of mimicry (Ali & Ripley 1983; Agnihotri et al. 2014, 2020). While
102 most studies on drongo vocalization have focused on the Greater Racket-tailed Drongo or the Fork-
103 tailed Drongo, there is no study on vocal behavior of the other drongo species that occur in
104 sympatry. Given their diverse vocal repertoire and their ability to learn and mimic other species-
105 in addition to being common forest birds- drongos present an ideal study system to understand
106 novel strategies for acoustic masking interference in a tropical forest site. This is additionally
107 pertinent because in forest habitats, the selective demand for acoustic communication is 'severe'
108 (Nemeth et al. 2001). For this study, we asked if a) drongos that occur in sympatry overlap in their
109 acoustic signal space and b) If they overlap in acoustic space, what strategies do drongos employ
110 to avoid other closely- related species?

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113 **Materials and Methods**
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115 ***Study site and species***
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117   We conducted the study in Dehing Patkai National Park and adjoining Jeypore Reserve
118 Forest (27°16'46.68"N, 95°29'32.91"E), in the Jeypore range of the Dibrugarh Forest Division in
119 the state of Assam, India from December 2018 to April 2019. The sanctuary covers an area of
120 111.19sq. km. The vegetation is classified as Assam Valley tropical evergreen forest (category
121 1B/C1) (Champion and Seth 2013) and is also part of the Dehing Patkai Elephant Reserve. The
122 sanctuary is the last stronghold of tropical lowland evergreen forests in the country. Important
123 species of flora include *Dipterocarpus artocarpus* (Hollong), *Shorea assamica* (Mekai), *Dillenia*
124 *indica*, *Mesua ferrea*, *Myristica limifolia*, *Castanopsis indica* (Jain et al. 2021).

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Fig 1: Dehing Patkai National Park is a lowland evergreen rainforest in Upper Assam, India. Figure also represents the four species of drongos studied and a spectrogram of their respective vocalizations; (Clockwise from top left: D. paradiseus (Greater Racket-tailed Drongo), D. remifer (Lesser Racket-tailed Drongo), D. aeneus (Bronzed Drongo), D. hottentottus (Hair-crested Drongo). Right: Tropical Rainforest of Dehing Patkai National Park. Photo credits: Sutirtha Lahiri, Abir Jain, Wikimedia commons.

We focused on drongos (Aves: Dicruridae), an insectivorous passerine found in tropical Asia, Africa, and Australia. Of the 29 species of drongos of the genus *Dicrurus*, 10 species occur in India (Grimmett et al. 1999). 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 the 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- *D. paradiseus*, *D. aeneus*, *D. remifer* and *D. hottentottus*. The Black Drongo is not found in sympatry with the other species in the study site; the Ashy Drongo, a winter migrant, was found in low numbers and never vocalized; and the Crow-billed Drongo, a possible summer migrant was encountered very rarely during the end of the field work. Hence, we did not collect data from these species. All fieldwork was done with appropriate permission from the forest department (permit no: WL/Fg.31/PT/Technical Committee/2018).

Recording

To record the different species of drongos, we walked trails in my field site between 6-10am and 13:30-16:30 when the activity period of birds was high. When we detected a drongo, we used a digital audio recorder (Zoom H4N) along with a Sennheiser ME66 unidirectional microphone and a K6 power module to record the vocalization of the individual. While recording, we also took notes of the perch height, the context of vocalization and the presence or absence of other species. We recorded the drongo for as long as they were within visible range. We recorded only when we were able to see the drongo to prevent any misidentification of calls, as there are

155   other birds like the Blue-winged Leafbird *Chlorpsis cochinchinensis* and the White-rumped Shama
156   *Copsychus malabaricus* which often mimic drongos. To avoid recording the same individual, we
157   recorded GPS coordinates and did not record in the same area on subsequent days.

158   For analyses of acoustic traits, we first digitized all the recordings in the software Raven
159   Pro 1.5.0 by drawing a selection box around each distinct note. We calculated 9 parameters from
160   the annotated notes: Note duration, 90% bandwidth, peak frequency, average entropy, peak
161   frequency at the start and end of the note (calculated using the peak frequency contour feature on
162   Raven Pro), peak time, maximum and minimum of the peak frequency contour (an overview of
163   these parameters is available in supplementary materials). We plotted the individual parameters
164   for each species.

165   To visualize the signal parameter space occupied by the drongo calls, we performed a
166   principal components analysis (PCA) on the correlation matrix for all parameters measured. A
167   correlation matrix is used if the units of measurements of the individual variables differ. To
168   quantify how different each drongo vocalizations are, we performed a linear discriminant analysis
169   (LDA) on the call notes (Total number of notes=3513). An LDA is a statistical tool to find the
170   maximum separation between clusters or classes. We trained a linear discriminant classifier on the
171   note parameters using the 'train' function in the R package 'Caret' (Kuhn 2008). We used this to
172   assess the accuracy with which the model correctly classifies each species. We generated a
173   confusion matrix to visualize this (Pheatmap package, Kolde & Kolde 2015). Species which are
174   distinct vocally will have a higher accuracy of being identified correctly. The analyses were done
175   in R (R core team 2021). Lastly, we performed a null model analysis to explore whether species
176   overlapped in signal space more or less than expected by chance (Chek et al. 2003). To do this, we
177   followed a null model test used in previous studies (Chitnis et al. 2020; Madabhushi 2023). For
178   this, we first took our first three PC scores, and randomly shuffled the species identity. For each
179   of the 1000 such randomized dataset, we calculated the interspecific Euclidean distance in signal
180   space. Finally, we compared the observed average interspecific distance to the distribution
181   obtained from the randomized dataset by computing a Z-score. If the song notes of drongos
182   overlapped in PC space, the observed interspecific distance in the PC space will be less than
183   expected by chance alone and the Z score would be significantly negative.

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Perch height

186   To understand whether drongos select different perch heights, we recorded perch heights
187   whenever we encountered a drongo. We estimated the height by a combination of both clinometer
188   (Suunto Tandem/360PC/360R DG clino/compass) as well as ocular estimation. Ocular estimation
189   was done- often in consultation with the local collaborator- only after calibrating with clinometer
190   measurements to ensure accuracy of estimation. These observations were done whenever we
191   sampled for acoustic recording, during transect walks, during vegetation sampling, or any *ad*
192   *libitum* sighting of drongos. Given the density of vegetation and the potential inaccuracy of height
193   measurements, we also undertook a conservative approach by categorizing heights into three broad
194   (and ecologically relevant) classes; lower canopy (0-5m), mid-canopy (6-22m), upper canopy
195   (22m and above) and analyzing the data for difference in perch height.

196   Following this, we clubbed separated song perch heights from perch heights where the
197   drongo was not vocalizing, and performed an ANOVA test to compare if song perch heights were

198   different in different species. We then performed a Tukey's HSD test to check for pairwise
199   differences in perch heights. We also calculated the proportion of the occurrence of each species
200   at each height category and performed a chi-square test. Finally, a pearson's correlation test was
201   conducted to check for correlation between peak frequency and mean perch height and built a
202   linear regression to obtain the line of best fit.

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204 **Results**
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206   We recorded a total of 84 individual drongos. Of this, we had a total of 3513 digitized notes
207   (*D. aeneus* N=936, *D. paradiseus* N=1248, *D. remifer* N=1094, *D. hottentottus* N=235). To
208   understand how differently the four species of drongos vocalize in sympatry, we use principal
209   components analysis. The first 2 principal components together explained 74.3% variation, while
210   the first 3 principal components together explained 86.8% of the variation in the data. The first
211   principal component loaded positively on frequency parameters, the second principal component
212   loaded positively on bandwidth and entropy measures, while the third loaded negatively for time
213   measures. The metrics are given in table 1. We also visualized the principal components to
214   qualitatively assess the extent of vocal overlap in the four species of drongos. (Fig 2). This was
215   further validated by our randomization test. We found that the average interspecific distance in the
216   note parameter space of *Dicruridae* is much lower (Z=-910.954, p<0.01) than expected by chance
217   alone, when we calculated it by randomizing PC scores 1000 times. Our linear discriminant
218   analysis further supported the high overlap in drongo vocalizations. The model performed poorly
219   when trying to discriminate between the different species, by having an accuracy of only 59%. The
220   highest classification rate for *D. paradiseus* (which occupied the opposite edges of the signal
221   space) was only ~29% (Fig 2). This analysis further supports the ordination results that drongos
222   overlap in their vocal space, and that there is very little partitioning in acoustic space.

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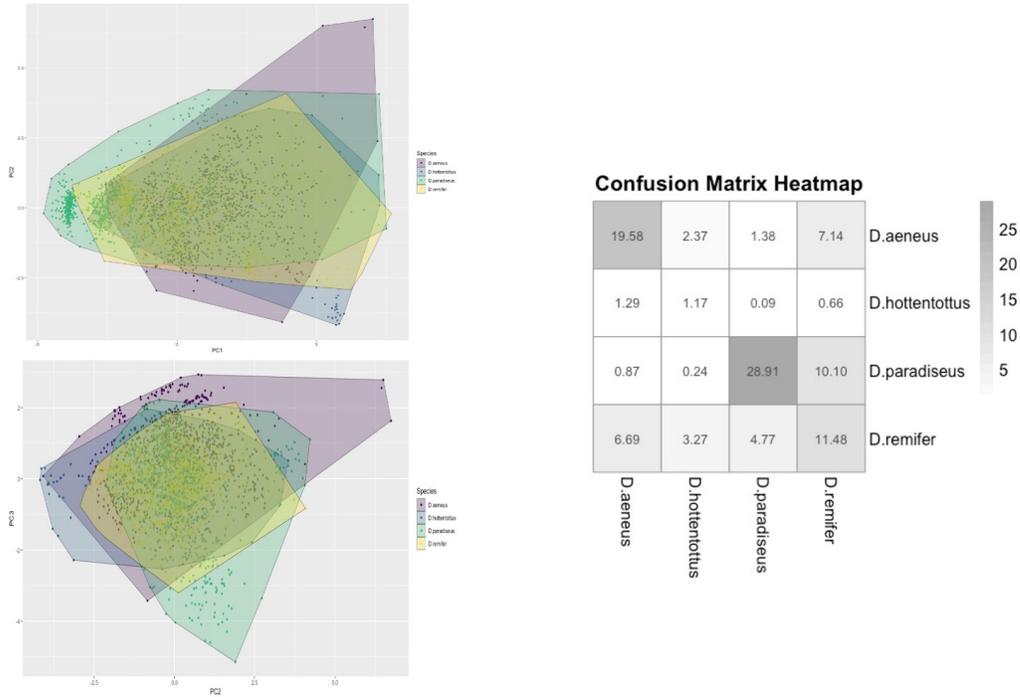
Fig 2: *The plots of PC scores represent high overlap between sympatric drongos (PC1 vs PC2, PC2 vs PC3). The confusion matrix (right) denotes high misclassification in the model predicting drongo species based on trained datasets on their acoustic parameters.*

For perch heights, we visualized heights both as boxplots as well as stacked bar plots for individual species (Fig 3). *D.hottentottus* occupied the highest perch, followed by *D.aeneus*. *D.remifer* and *D. paradiseus* occupied the same median heights. The ANOVA test was significant (F=87.27, p<2.2e-16) for the four species of drongos and held true even when we considered only perches where we recorded the bird vocalizing. The test also met the underlying assumptions of ANOVA, i.e.-homogeneity of variance (Residual vs fitted plot) and normality of data (Q-Q plot) (Supplementary figure S1). Tukey's HSD test was significant for all pairs of species, except for LRT and GRT (p=0.9853).

When we clubbed the data into discrete height categories and performed a chi-square test, we similarly found a significant difference in perch heights in drongos (X-squared = 199.76, df = 6, p-value < 2.2e-16). *D.remifer* vocalized from the mid-storey ~80% of the time, *D.hottentottus* vocalized from the upper-storey >94% of the time, while *D.paradiseus* vocalized mostly from the mid-storey (~64%) (Table S3). While perch height and peak frequency were correlated, this was not significant.

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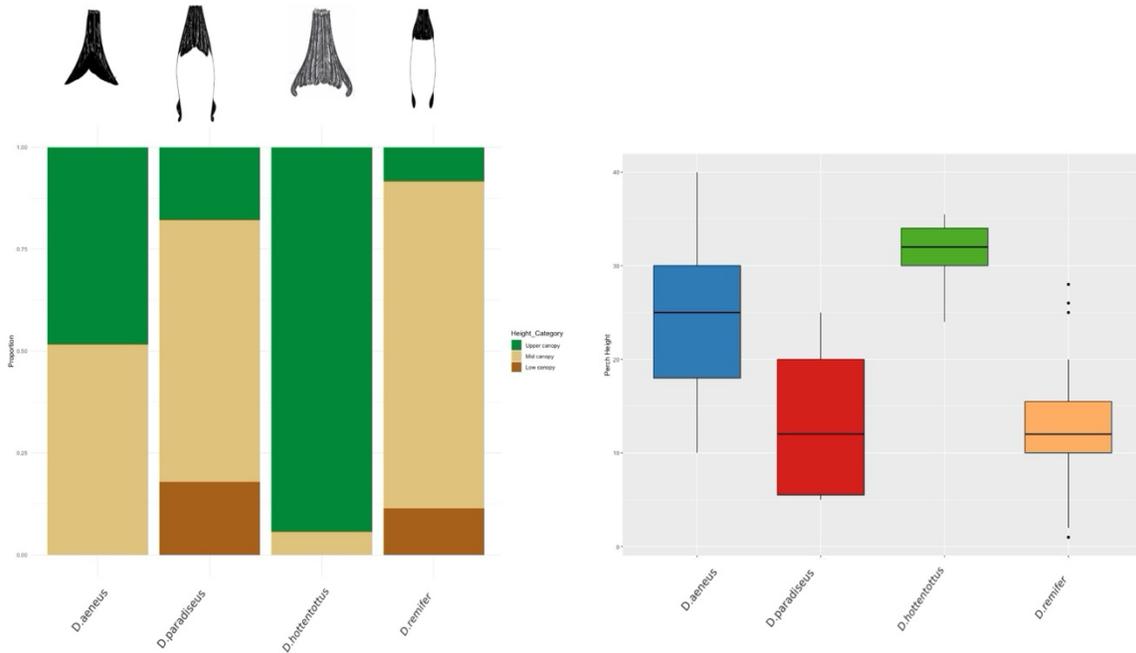
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259 *Fig 3: Perch heights in the four species of drongo. Perch height was quantified both as discrete*
260 *(lower, mid, and upper canopy) and as a continuous value. Drongos segregate in perch heights,*
261 *with D. Hottentottus occupying the highest perch, and D. paradiseus the lowest.*

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Discussion

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266   In this paper, we report on the high vocal overlap in sympatric drongos of the lowland
267 evergreen forests of East India. We find that the four species of drongos, when occurring in
268 sympatry, do not have distinct clusters in their acoustic space. However, we find evidence of
269 drongos separating in their perch heights. Below, we expand on how these findings, taken together,
270 provide new insights on the vocal behavior of sympatric birds.

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272 Vocal space overlap

For acoustically communicating species, the acoustic channel can be regarded as an acoustic resource (Schmidt & Balakrishnan 2015), and with many 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, temporal, and spatial properties. There is multiple evidence of vocal partitioning in sympatric bird species, such as barbets (Krishnan & Tamma 2016), wren-warblers(Chitnis et al. 2020), cuckoos (Mei et al. 2023). Partitioning in acoustic space is thought to play a role in avoiding masking interference among closely related species and promote unambiguous species recognition to avoid hybridization and reproductive failure (Seddon 2005).

However, our study revealed the opposite. We show evidence of overlap in the multidimensional acoustic space between the four species of drongo (fig 2). Overlaps in the acoustic space of drongos are suggestive of the breadth of auditory capabilities the species can extend to. One reason for this overlap in their acoustic signal space is the ability of drongos to mimic other species (Ali & Ripley 1983; Grimmett et al. 1999). Owing to the plasticity of their vocalization and in particular, their capability of mimicking other species, drongos have a high diversity of notes in their repertoire (Agnihotri et al. 2014), unlike species which do not learn their calls like suboscines. Indeed, mimicry in passerines is not uncommon and occurs in almost 20% of bird species which learn their vocalization. By mimicking other species, drongos can potentially exploit a much larger fundamental acoustic space. Mimicry in *D. paradiseus* has been documented to serve several social and highly contextual functions like attracting mix-flocks (Goodale & Kotagama 2006), alarm calling, mobbing (Goodale & Kotagama 2005), kleptoparasitism (Satischandra et al. 2010; Flower 2010) in addition to mate attraction and territorial defense (Dalziell et al. 2015). In the African fork-tailed drongo *D.adsimilis*, experiments found that mimicking species-specific and heterospecific alarm calls made other birds abandon their food, which was simultaneously stolen by the drongo (Flower 2010). However, one of the most comprehensive pieces of evidence for the function of mimicry in drongos come from their role in facilitating heterospecific mix-flocks. Attracting a mixed flock is of particular importance for a drongo, as it increases foraging efficiency (Satischandra et al. 2007). In a study in Sri Lanka, it has been noted that the *D. paradiseus* 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 mixed flock being present, and thus deceives the birds to form a flock (Goodale & Kotagama 2006). Although anecdotal, this was observed in the case of *D.remifer* as well, which also forms and forages in mix flocks (Dhanasarnpaiboon & Round 2004) and mimicked species like the Sultan Tit *Melanochlora sultanea* and the White-throated Bulbul *Alophoixus flaveolus*- both species which were observed as members of mixed flocks with *D.remifer* (Fig 5). Our study, thus, potentially theorizes about mimicry in drongos as a reason for a broad vocal repertoire and simultaneous overlap in acoustic space of sympatric drongos. Similar results have been found in two species of drongos- *D. paradiseus* and *D.lophorinus (*Or *D.p.lophorinus*), where authors found evidence for wide overlap, owing to both vocal plasticity and repertoire complexity (Weerakkody et al. 2023). Overlap in acoustic space is not limited to drongos and are, in fact, reported in several other species like *Ficedula* flycatchers (Haavie et al. 2004) and *Streptopelia* doves (De Kort et al. 2002). Our study also suggests further exploration of mimicry in drongos, especially the patterns and sequences of the vocal repertoires as a possible means to overcome masking interference between sympatric drongos. Indeed, while signal space might overlap, birds can have different strategies to overcome masking. For example, a recent study in allopatric montane wren-babblers (*Spelaeornis*) found that while signal space overlaps in the different species, they can segregate by

319   having divergent song note sequences (Madabhushi et al. 2023). Given the interspersed mimetic
320   and species-specific call notes in the repertoire of drongos, exploring the vocal sequences in
321   sympatric drongos may shed light on segregation in spectral dimensions. In our field site *D.*
322   *paradiseus*, we have observed rapid mimicry of different species of birds in one bout, followed by
323   drongo-specific calls, which contrasts with our observation of the other drongos which have more
324   regular interspersed mimetic and species-specific calls.
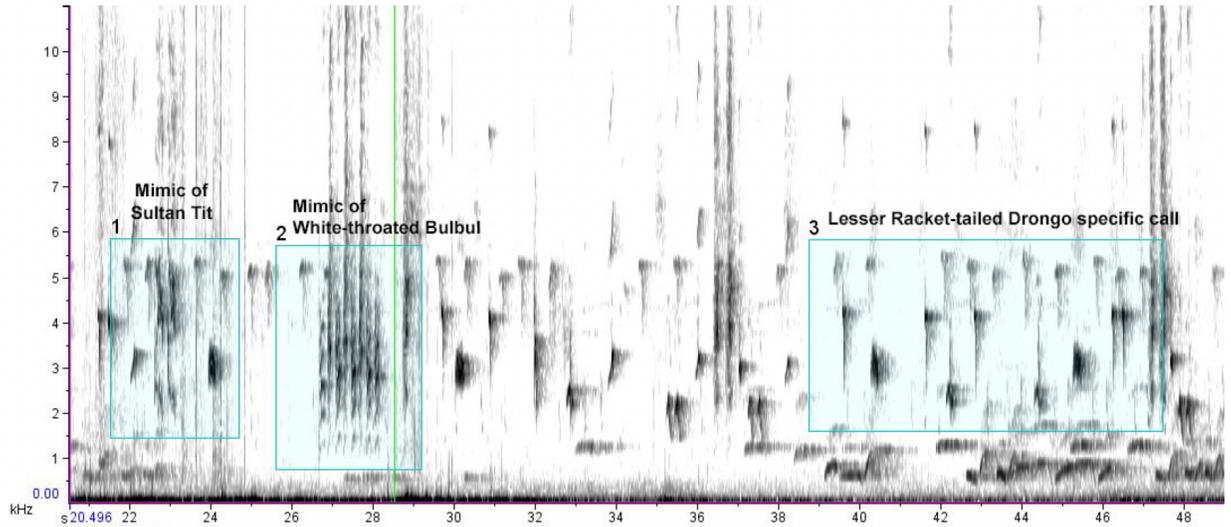
326   Fig 4: Mimicry of Sultan Tit and White-throated Bulbul by the *D. remifer*.

Perch heights

329   Song post heights are an important adaptation to counteract the effect of habitat on the
330   acoustic trait of a species and is well documented in diverse animal taxa. In insects in a tropical
331   evergreen forest, species segregated in their song perch heights (Diwakar & Balakrishnan 2007)
332   and birds (Nemeth et al. 2001; Seddon 2005). Transmission studies have found how greater heights
333   offer better transmission and broadcast area (Ellinger & Hödl 2003; Jain & Balakrishnan 2012).
334   For example, studying a group of Venezuelan Antbirds, there is evidence of optimal transmission
335   from perch heights, suggesting that birds might be selecting specific perches for optimal
336   transmission of signals. The mid-storey comes as the best suited height for vocalizing animals,
337   because of the dual advantage of lesser foliage density and height above the ground (Schmidt &
338   Balakrishnan 2015). However, very few animals use this stratum because of increased detectability
339   by predators.

340   In this study, we find evidence of significant difference in the mean song perch heights
341   between the four species of drongos (Figure 3). *D.hottentottus* occupies the highest mean perch
342   height (31.5±2.6m), followed by *D.aeneus* (24±7.27m). *D. paradiseus* (12.42±6.8 m) and
343   *D.remifer* (13±5.9m), however, have no significant difference in their mean song perch heights.
344   Our results hold even when we do a similar analysis with the conservative height classes. Similar
345   patterns of vertical stratification have been seen in drongos in an evergreen and moist deciduous
346   forest of Thekkady in Kerala (Vijayan 1984) and Assam (Nath et al. 2016), where the *D.aeneus*
347   occupied the higher strata while the *D. paradiseus* favored the lower strata. During our study, we

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observed drongos forage with unique mix-flock groups; while the *D.aeneus* typically foraged with higher strata species including different species of *Pericrocotus sp.* (minivets), mid elevation drongo like *D.remifer* associated with birds like the Sultan tit and white-throated bulbul. Since mimicry in drongos are important to attract mixed flocks, the selection of different perch heights might be associated with acoustic considerations. As mixed flocks are themselves stratified in a forest (Robin et al. 2002; Sridhar et al. 2012) with different flock types occupying different strata of the forest, drongos (which are known to be nuclear species that help form flocks) likely segregate in height in response to flock types.

One reason for the *D. paradiseus* and *D.remifer* to occupy similar song post height is that they are more closely related to one another than to other drongo species in the study area (Pasquet et al. 2007). Additionally, they are also similar in their morphology (Ali & Ripley 1983) which might explain their preference for a similar perch height. *D.remifer* and *D. paradiseus* were also opportunistically seen foraging in mixed flocks with similar participant species, thereby suggesting the possibility of overlap in perch heights. The song perch height of the *D. hottentottus*, being the highest, is likely also because they are nectarivores (Ali and Ripley 1983) and thus always occupied the higher perches of flowering trees like *Bombax ceiba* and *Erythrina spp*. We always recorded *D. hottentottus* only when the species was present in either of these trees.

Many studies have also shown how different perch heights are optimized for particular frequencies to efficiently transmit (Nemeth et al. 2001; Seddon 2005). Species in the lowest strata- with higher vegetation density- will have the lowest frequency (which will allow it to travel longer distances with minimal transmission loss), while upper canopy species will have higher frequency (Catchpole and Slater 2003). In the four species of drongo, the *D. hottentottus*, which occupies the highest perch (31.5±2.6m) also has the highest peak frequency (3565.3±272.31Hz), while the *D. paradiseus*, which occupies the lowest height (12.42±6.8 m) has the lowest peak frequency (2407.3±392.16Hz). This relation was, however, not significant and should thus be interpreted with caution. Determining a relationship between song parameters and perch heights would require additional sound transmission studies to determine if song parameters from a given perch are best suited for that height. These studies can also tease apart whether perch height segregation occurs due to acoustic constraints or other ecological factors such as competition for perch and predation pressure. Our results, however, underscore the complexity of vocal behavior in the Eastern Indian lowland evergreen forests, which has one of the highest avian diversities on Earth (Saikia & Devi 2011; Lahiri & Sonowal 2020; Jain et al. 2021). Our data suggests potential segregation in the multidimensional signal space by segregating in perch height when there is overlap in spectral space owing to diverse vocal repertoire in drongos. The evergreen forests of Eastern India are home to groups of birds that are closely related and co-occurring, which permits the potential for future studies that explore the strategies they employ to segregate in the multidimensional signal space.

Acknowledgement

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