

1 **Simultaneously vocalizing Asian barbets adopt different frequencies without**
2 **coordinating temporal rhythms**

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7 **Running title:** Vocal rhythms of Asian barbets

8 **Keywords:** Barbet, duet, frequency, sound stream segregation, vocal coordination

9

10 **Abstract**

11 Sound stream segregation is an important challenge faced by simultaneously vocalizing
12 animals. Chorusing birds, for instance, coordinate vocal timing to minimize overlap.
13 Alternatively, other birds may use frequency differences to segregate sound streams, and
14 vocalizing at different frequencies may enable them to remain distinct from each other. Here, I
15 show that conspecific Asian barbets vocalize at distinctly different peak frequencies from each
16 other. Additionally, they also differ in repetition rate, as measured by the inter-phrase interval.
17 However, conspecific individuals across species do not temporally coordinate with each other
18 during vocal interactions, maintaining independent and highly stereotyped individual rhythms
19 together with different peak frequencies. Frequency differences between individuals may
20 facilitate sound stream segregation when calls overlap in time. I propose that frequency
21 differences between conspecifics may be widespread among birds possessing stereotyped,
22 repetitive calls such as those found in barbets. This may enable segregation of competing
23 sound streams both during cooperative duets and competitive singing during territorial
24 interactions.

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28 **Introduction**

29 Animal choruses represent a striking natural example of the ‘cocktail party problem’, where
30 individuals must segregate relevant information from competing streams of sound, both
31 conspecific and heterospecific (Bee and Micheyl, 2008; Greenfield, 1994). This applies both to
32 territorially singing males, and birds singing agonistically together in duets (Hall, 2004; Hall,
33 2009). In both scenarios, conspecific individuals must emit distinct signals in order to
34 communicate with each other. Vocalizing at differing frequencies (Krishnan and Tamma, 2016;
35 Narins, 1995; Nityananda and Bee, 2011), or altering vocal timing (Brumm, 2006; Cody and
36 Brown, 1969; Fleischer et al., 1985; Luther, 2008) may minimize masking interference from
37 overlapping sounds. Some birds are known to simply sing together without temporal
38 coordination, and their vocalizations drift in and out of phase with each other (Hall, 2009; Payne
39 and Skinner, 1970). As a result, simultaneously vocalizing conspecifics may repeatedly overlap
40 in time, depending on the differences in repetition rate. In such cases, frequency differences
41 may assume greater importance in sound stream segregation (MacDougall-Shackleton et al.,
42 1998). By recording animal choruses and isolating the frequencies and repetition rates of each
43 individual, we may obtain an indication into how each individual may be able to distinguish
44 themselves over a chorus of conspecifics.

45 Here, I describe the vocal strategies employed by Asian barbet (Piciformes: Megalaimidae)
46 (Short and Horne, 2001) choruses in India. Across Asia, multiple species of sympatric barbet
47 co-occur, each vocalizing in a species-specific frequency band (Krishnan and Tamma, 2016). In
48 addition to these interspecific differences, multiple individuals of the same species frequently
49 vocalize together in choruses (Ali and Ripley, 1997; Short and Horne, 2001). However, the
50 mechanisms that barbets employ to segregate their signals from conspecifics remain poorly
51 understood. By studying simultaneously vocalizing conspecifics of four different species, I aimed
52 to preliminarily understand whether vocal patterns were similar or diverse across the family. My

53 study examined whether simultaneously vocalizing conspecific barbets of each species
54 segregate from each other either in vocal peak frequencies, or by coordination of vocal timing.
55 For this, I examined whether conspecifics vocalizing together differed in peak frequency and
56 repetition rates, and then examined the inter-phrase intervals between two conspecific
57 individuals to elucidate whether, across species, there was any evidence that barbets
58 coordinated their calls with respect to vocal conspecifics. Understanding the vocal strategies
59 employed by these non-passerine birds enables a broader understanding of the diversity of
60 animal strategies to minimize acoustic masking.

61

62 **Materials and Methods**

63 *Recording*

64 I recorded barbet choruses in the city of Pune in Maharashtra (Peninsular India), and the village
65 of Mandal in Uttarakhand (Western Himalayas) in March-April 2018, early in the breeding
66 season. Each site houses two species of barbet, *Psilopogon viridis*/*P. haemacephalus* in Pune,
67 and *P. virens*/*P. asiaticus* in Mandal (Figure 1A. For recordings, I used Sennheiser (Wedemark,
68 Germany) ME62 omnidirectional microphones connected to a Zoom H6 (Tokyo, Japan) recorder
69 sampling at 44.1KHz, making note of multiple simultaneously vocalizing conspecific individuals.
70 The recorder and microphones were stationary on the ground to avoid movement noise. The
71 overall dataset consisted of approximately seven hours of barbet chorus recordings.

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73 *Analysis*

74 Using Raven Pro 1.5 (Cornell Laboratory of Ornithology, Ithaca, NY, USA), I digitized
75 vocalizations of barbets from each recording and calculated peak frequencies of each note (PF,
76 using an FFT window size of 2048 for higher frequency resolution of small differences) as well
77 as the inter-phrase interval (IPI, the time gap between the end of one phrase and the beginning
78 of the next, using a window size of 512 for higher resolution of small timing differences). For

79 each species, I digitized approximately 2500 individual phrases (1-5 notes/phrase depending on
80 the species). I listened to all recordings using headphones while labeling vocalizations,
81 differentiating conspecific individuals by the differences in relative amplitude (birds that were
82 further from the microphone were lower-amplitude in recordings, and distinguishable in Raven
83 Pro). First, I examined whether two simultaneously vocalizing conspecific individuals differed in
84 PF and IPI, using paired Wilcoxon signed-rank tests. Next, I measured the interquartile range or
85 IQR of IPI (for 108 total instances of a vocal barbet across all four species), to quantify
86 stereotypy in temporal rhythms. Secondly, to examine whether simultaneously vocalizing
87 conspecifics (36 instances across four species, an instance defined as bouts of vocalizations
88 from the same individual without long gaps; this was the most conservative way to identify
89 behavioral instances given that I could not identify individual birds in the field) were temporally
90 synchronous or asynchronous with each other, I calculated the time lag between the beginning
91 of each phrase of one individual and the closest call of the other using MATLAB (Mathworks
92 Inc., Natick, MA, USA). If birds were synchronous, I predicted that the distribution of time lags
93 across a bout should show a clear peak and low coefficient of variation (i.e. a stereotypical time
94 lag between individuals) (Taylor et al., 2019). However, an asynchronous bout would imply
95 independent rhythms from each other; the two individuals would thus drift in and out of phase,
96 resulting in a uniform distribution of time lags. For each instance with 5 or more measured time
97 lags (27 in total), I performed two-sample Kolmogorov-Smirnov tests against 100 randomly
98 generated uniform distributions spanning the same range of values. I scored the results as 0 if
99 they did not differ significantly from uniform ($P > 0.05$), or 1 if they did ($P < 0.05$), and measured
100 the percentage of total 1's (out of 100 tests) for each of the 27 instances. A score of 0 for an
101 instance indicated a uniform distribution of time lags consistent with independent temporal
102 rhythms, and a score of 1 indicated a constant time lag consistent with two birds singing in
103 coordination.

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108 **Results**

109 *Conspecific barbets sing at different frequencies and repetition rates*

110 PF-IPI probability density plots revealed intraspecific variation in PF and IPI (Figure 1B, see
111 supplementary videos for 3D rotations). For example, in *P. haemacephalus*, two distinct peaks
112 were consistent with two distinct types of song, one at about 0.7KHz with an IPI at
113 approximately 0.5s, and a slower song at approximately 0.95KHz with an IPI over 1s (total of 27
114 measured instances). For *P. viridis*, I observed a similar bimodal distribution with variation
115 (difference between minimum and maximum) of over 130Hz in PF and over 1.3s in IPI (total of
116 65 measured instances). For *P. virens* and *P. asiaticus*, my data likely involved a long series of
117 measurements from relatively few individuals. Thus, although I digitized a similar number of
118 phrases in these species, these were separable into only 9 and 7 separate behavioral
119 instances, respectively. Although this sample size was too small to construct probability density
120 distributions, the measured PF and IPI exhibited high intraspecific variation (maximum-
121 minimum) for both species: 116Hz PF and 0.23s IPI variation for *P. virens*, and 148Hz PF and
122 0.04s IPI variation for *P. asiaticus* (although IPI variation was small in the latter species, there
123 was a consistent difference in the few cases when two individuals were vocalizing together,
124 even across very long bouts, as discussed in the next section). Intraspecific PF and/or IPI
125 variation was thus broadly consistent across all four species, suggesting that simultaneously
126 vocal conspecifics may adopt different frequencies and/or repetition rates from each other.

127 To statistically test this assertion, I compared the PFs and IPIs of simultaneously vocal barbets
128 using paired Wilcoxon signed-rank tests. Because the data for *P. virens* and *P. asiaticus*
129 consisted mainly of very long interactions across relatively few individuals (therefore, a very
130 large number of labeled notes, but few individual instances of simultaneously vocal barbets), I

131 performed this analysis only for *P. viridis* (N=22 instances of two barbets vocalizing together)
132 and *P. haemacephalus* (N=8). In both species, tests revealed significant (*P. viridis*: IPI: signed
133 rank= 253, $P < 0.001$, PF: signed rank= 256, $P < 0.001$, *P. haemacephalus*: IPI: signed rank= 36,
134 $P < 0.01$, PF: signed rank= 36, $P < 0.01$). This suggests that intraspecific variation in the
135 measured time and frequency parameters resulted from conspecific individuals adopting
136 different frequencies and vocal rhythms from each other. This can be seen in Figure 2A, where
137 the spectrograms clearly show conspecifics vocalizing at different frequencies and repetition
138 rates.

139

140 *Simultaneously vocalizing conspecifics sing at independent rhythms without synchronization*

141 I next sought to establish whether vocally interacting conspecific barbets adjusted their
142 repetition rates to maintain synchrony with their vocal neighbors. Across 36 instances of
143 simultaneously vocalizing conspecifics, I calculated the time lags between the calls of two
144 individuals (Figure 2A). For this, I used data from all four species, as there were enough
145 individual vocalizations digitized for the sample size of total time lag values to be sufficient for
146 statistical analysis. The time lags between the calls of two individuals had very high coefficients
147 of variation for each species (*P. haemacephalus*: 144.13%, *P. viridis*: 164.52%, *P. virens*:
148 182.55%, *P. asiaticus*: 197.11%), supporting a lack of vocal timing coordination (Hall, 2009).
149 Time lags exhibited a range of values across all 4 species, as opposed to a single value that
150 would be expected if two individuals coordinated vocal timing by phase-locking (Figure 2B).
151 When compared to 100 randomized uniform distributions (this was done for each of 27
152 instances, see Methods), time lags fit a uniform distribution 92% of the time on average
153 (average score 0.08, $P > 0.05$, Supplementary Data, Figure 3A, also see Methods). This uniform
154 distribution of time lags, together with high CVs, thus supports barbets vocalizing with
155 independent temporal rhythms rather than synchronizing with each other. In further support of
156 this, each barbet maintained its individual rhythm, whether vocalizing alone or with conspecifics.

157 The probability density plot of IQRs for the IPI of each individual barbet (all individual behavioral
158 instances measured, either solo or with another barbet) peaked at 47ms (Figure 3B), indicating
159 <50ms jitter in vocal timing across all species (including measurement-related variation). This
160 analysis included every individual instance of a vocal barbet across the dataset (solo and with
161 other conspecifics), in spite of which I observed a sharp peak indicating a precise vocal rhythm.
162 This further supports the idea that barbets maintain stable, independent vocal rhythms
163 regardless of whether they vocalize solo or with conspecifics.

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165 **Discussion**

166 Avian vocal interactions have received much study for the precisely coordinated vocal timing
167 between individuals; many of these studies have focused on duetting birds (Fortune et al., 2011;
168 Hall, 2009), but others have also focused on temporal asynchrony of songs to minimize overlap
169 (Cody and Brown, 1969; Fleischer et al., 1985). However, other birds exhibit independent
170 temporal rhythms with no phase-locking or coordination between simultaneously vocalizing
171 individuals (Hall, 2009). My data suggests that Asian barbets do not coordinate vocal timing with
172 respect to other vocal conspecifics, and I also find that simultaneously vocalizing individuals
173 tend to differ in the peak frequencies of their vocalizations. If two barbets vocalize at
174 independent and different rhythms, their vocalizations will drift in and out of phase with each
175 other (resulting in a uniform distribution of time lags between the two individuals, as opposed to
176 the single peak one might expect if they were coordinated with each other).

177 Dilger (Dilger, 1953) described simultaneous singing in *P.haemacephalus* involving both
178 members of a pair vocalizing at different frequencies. My dataset, consisting of broad passive
179 recordings of barbet choruses, presumably consists of a mix of vocal individuals, both vocal
180 pairs and territorial countersinging birds. This, of course, assumes that both members of a pair
181 sing across species as per Dilger's observations, which requires further study. Because barbets
182 are often difficult to locate when singing, usually high up in the canopy, and the sexes are alike,

183 it is extremely challenging to identify individual birds. However, at the species-level, I find that
184 conspecific individuals vocalize together with differences both in peak frequency and the interval
185 between phrases. Additionally, in no instance do I find evidence of birds changing their temporal
186 rhythms to minimize overlap. Instead, barbets appear to simply adopt different temporal rhythms
187 from each other, which may involve paying attention only to the start of another bird's bout.
188 Although different repetition rates may reduce temporal overlap to some extent, some
189 vocalizations of two individuals will still overlap in time. In this case, frequency differences
190 between individuals may support sound stream segregation (MacDougall-Shackleton et al.,
191 1998; Nityananda and Bee, 2011). Frequency differences between conspecifics are smaller
192 than those between heterospecifics (Krishnan and Tamma, 2016), suggesting that they serve to
193 differentiate individuals within each species' frequency band.

194 Some species of the related African barbets (*Lybiidae:Trachyphonus*) pair-duet, and certain
195 species appear to exhibit vocal timing coordination (Horne and Short, 1983; Thorpe, 1963).
196 However, duetting partners in other species may exhibit independent rhythms (Payne and
197 Skinner, 1970). It is thus possible that Asian barbets may sometimes coordinate their rhythms
198 over short time scales, although my study does not uncover evidence of this. By and large, the
199 evidence I present suggests that frequency differences between conspecifics are more
200 important than temporal mechanisms to minimize vocal overlap. Similar mechanisms may also
201 operate in other non-passerine birds such as the pheasant-coucal, where simultaneously
202 vocalizing members of a pair exhibit different frequencies (Maurer et al., 2008). Comparative
203 study may thus help us understand the diversity of strategies employed by birds to minimize
204 masking interference when singing in a chorus.

205

206 **Acknowledgments**

207 I thank Rohit Chakravarty, Zareef Khan, Baseer Baniya and Arun Varghese for assistance
208 during recordings, Raghav Rajan and his lab for inputs on the data, Samira Agnihotri and
209 Shivam Chitnis for discussions on analysis.

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214 **Funding**

215 My research is funded by an INSPIRE Faculty Award from the Department of Science and
216 Technology, Government of India and an Early Career Research (ECR/2017/001527) Grant
217 from the Science and Engineering Research Board (SERB), Government of India.

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219 **References**

220 **Ali, S. and Ripley, S. D.** (1997). *Handbook of the Birds of India and Pakistan, Volume 4:*

221 *Frogmouths to Pittas*. 2nd Editio. New Delhi: Oxford University Press.

222 **Bee, M. A. and Micheyl, C.** (2008). The “Cocktail Party Problem”: What is it? How can it be
223 solved? And why should animal behaviorists study it? *J. Comp. Psychol* **122**, 235–251.

224 **Brumm, H.** (2006). Signalling through acoustic windows: Nightingales avoid interspecific
225 competition by short-term adjustment of song timing. *J. Comp. Physiol. A Neuroethol.*

226 *Sensory, Neural, Behav. Physiol.* **192**, 1279–1285.

227 **Cody, M. L. and Brown, J. H.** (1969). Song asynchrony in neighbouring bird species. *Nature*
228 **222**, 778–780.

229 **Dilger, W. C.** (1953). Duetting in the Crimson-breasted barbet. *Condor* **55**, 220–221.

230 **Fleischer, R. C., Boarman, W. I. and Cody, M. L.** (1985). Asynchrony of song series in the
231 Bewick’s wren and wren tit. *Anim. Behav.* **33**, 674–676.

232 **Fortune, E. S., Rodríguez, C., Li, D., Ball, G. F. and Coleman, M. J.** (2011). Neural

- 233 mechanisms for the coordination of duet singing in wrens. *Science* (80-.). **334**, 666–670.
- 234 **Greenfield, M. D.** (1994). Synchronous and alternating choruses in insects and anurans:
235 Common mechanisms and diverse functions. *Integr. Comp. Biol.* **34**, 605–615.
- 236 **Hall, M. L.** (2004). A review of hypotheses for the functions of avian duetting. *Behav. Ecol.*
237 *Sociobiol.* **55**, 415–430.
- 238 **Hall, M. L.** (2009). Chapter 3 A Review of Vocal Duetting in Birds. *Adv. Study Behav.* **40**, 67–
239 121.
- 240 **Horne, J. F. M. and Short, L. L.** (1983). A Review of Duetting, Sociality and Speciation in
241 Some African Barbets (Capitonidae). *Condor* **85**, 323–332.
- 242 **Krishnan, A. and Tamma, K.** (2016). Divergent morphological and acoustic traits in sympatric
243 communities of Asian barbets. *R. Soc. Open Sci.* **3**, 160117.
- 244 **Luther, D. A.** (2008). Signaller: receiver coordination and the timing of communication in
245 Amazonian birds. *Biol. Lett.* **4**, 651–654.
- 246 **MacDougall-Shackleton, S. A., Hulse, S. H., Gentner, T. Q. and White, W.** (1998). Auditory
247 scene analysis by European starlings (*Sturnus vulgaris*): perceptual segregation of tone
248 sequences. *J. Acoust. Soc. Am.* **103**, 3581–3587.
- 249 **Maurer, G., Smith, C., Süsser, M. and Magrath, R. D.** (2008). Solo and duet calling in the
250 pheasant coucal: sex and individual call differences in a nesting cuckoo with reversed size
251 dimorphism. *Aust. J. Zool.* **56**, 143–149.
- 252 **Narins, P. M.** (1995). Frog Communication. *Sci. Am.* **273**, 78–83.
- 253 **Nityananda, V. and Bee, M. A.** (2011). Finding your mate at a cocktail party: Frequency
254 separation promotes auditory stream segregation of concurrent voices in multi-species frog
255 choruses. *PLoS One* **6**,.
- 256 **Payne, R. B. and Skinner, N. J.** (1970). Temporal patterns of duetting in african barbets. *Ibis*
257 (*Lond. 1859*). **112**, 173–183.
- 258 **Short, L. . and Horne, J. F. M.** (2001). *Toucans, Barbets and Honeyguides*. Oxford Univ.

259 Press.

260 **Taylor, C. J., Hall, M. L., Cain, K. E. and Langmore, N. E.** (2019). A superb solo, or a deviant
261 duet? Overlapping songs in superb fairy-wrens. *Behav. Ecol.* **30**, 1076–1086.

262 **Thorpe, W. H.** (1963). Antiphonal singing in birds as evidence for avian auditory reaction time.
263 *Nature* **197**, 774–776.

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266 **Figure legends**

267 **Figure 1: A.** Spectrograms of barbet vocalizations from Peninsular India (left) and the Western
268 Himalayas (right). **B.** Three-dimensional probability density distributions indicating the
269 occurrence of different mean PF and repetition rates (IPI) for *P.haemacephalus* and *P.viridis*.

270

271 **Figure 2: A.** Spectrograms of two simultaneously vocalizing *P.viridis* (left) and
272 *P.haemacephalus* (right), demonstrating intraspecific differences in frequency and repetition
273 rate. The white bars represent the time lag between two individuals; note how it changes with
274 each repetition. **B.** Graphs of all measured values of time lag between two individuals for each
275 species of barbet. The longer the horizontal bar, the longer the time lag; the y-axis represents
276 the number of such measurements made per species. Values vary from approximately 100ms
277 to over a second, indicating a lack of temporal synchrony between individuals.

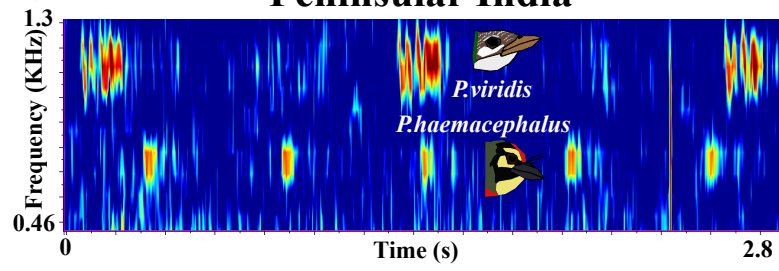
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279 **Figure 3: A.** Proportion of 100 Kolmogorov-Smirnov tests in which the observed distribution of
280 time lags differed from a random uniform distribution (for 27 instances of two conspecific
281 barbets vocalizing together). In 18/27 cases, the observed distribution fit >90% to a uniform
282 distribution (x-axis values <0.1, indicating independent temporal rhythms without synchrony).
283 Almost all other instances also fit well to a uniform distribution (the lowest being a 59% fit to
284 uniform, x-axis value 0.41), again supporting independent vocal rhythms. **B.** Distribution of IQRs

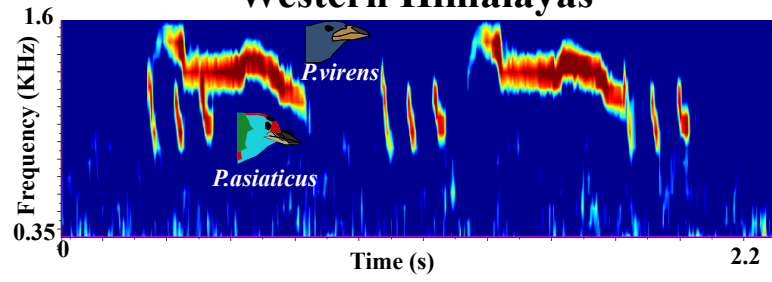
285 for the IPI of each individual instance of a vocalizing barbet across the entire dataset (both solo
286 and simultaneous calling, N=108). The peak at 47ms indicates very low IQRs, and therefore a
287 highly stereotyped temporal rhythm regardless of whether the barbet is vocalizing solo or with
288 conspecifics.

A

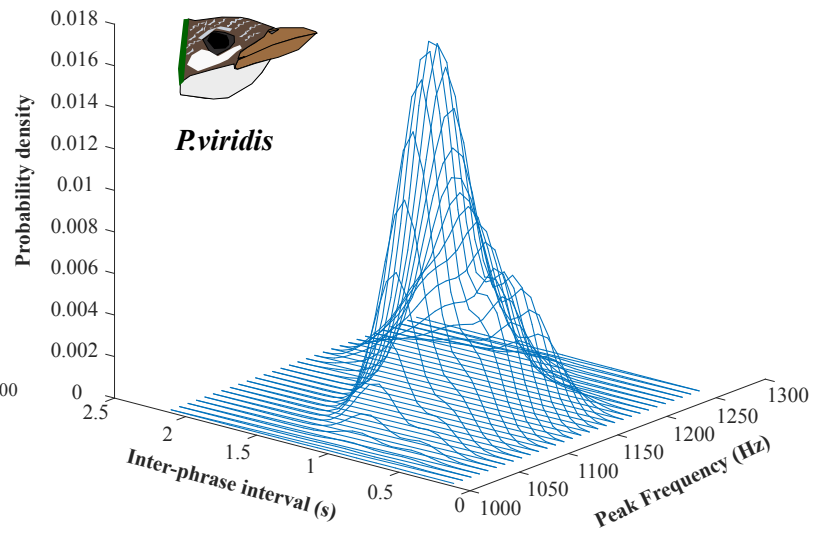
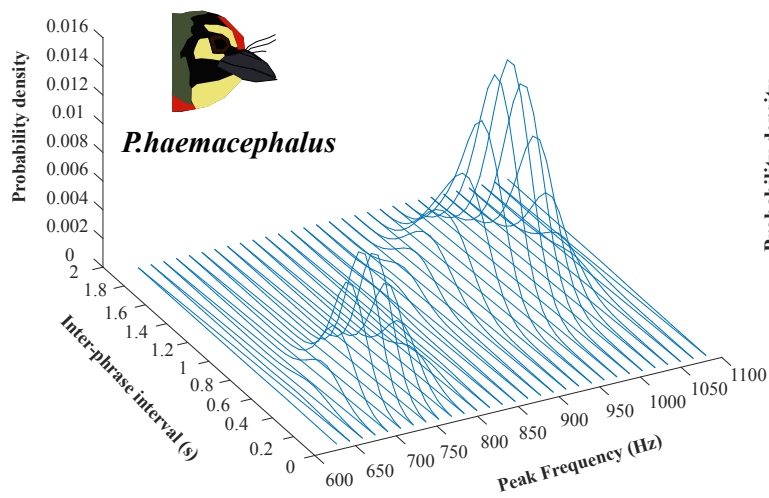
Peninsular India

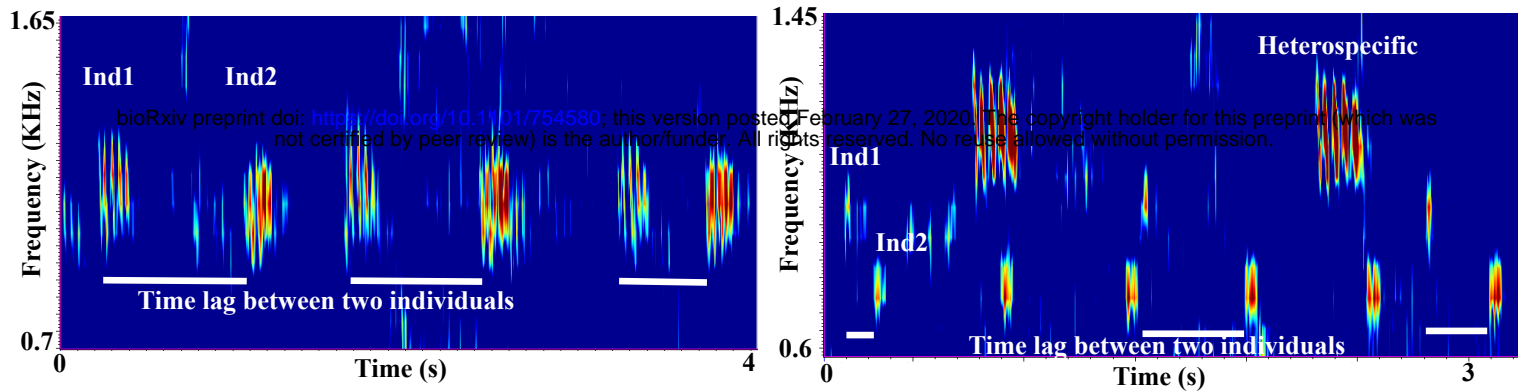
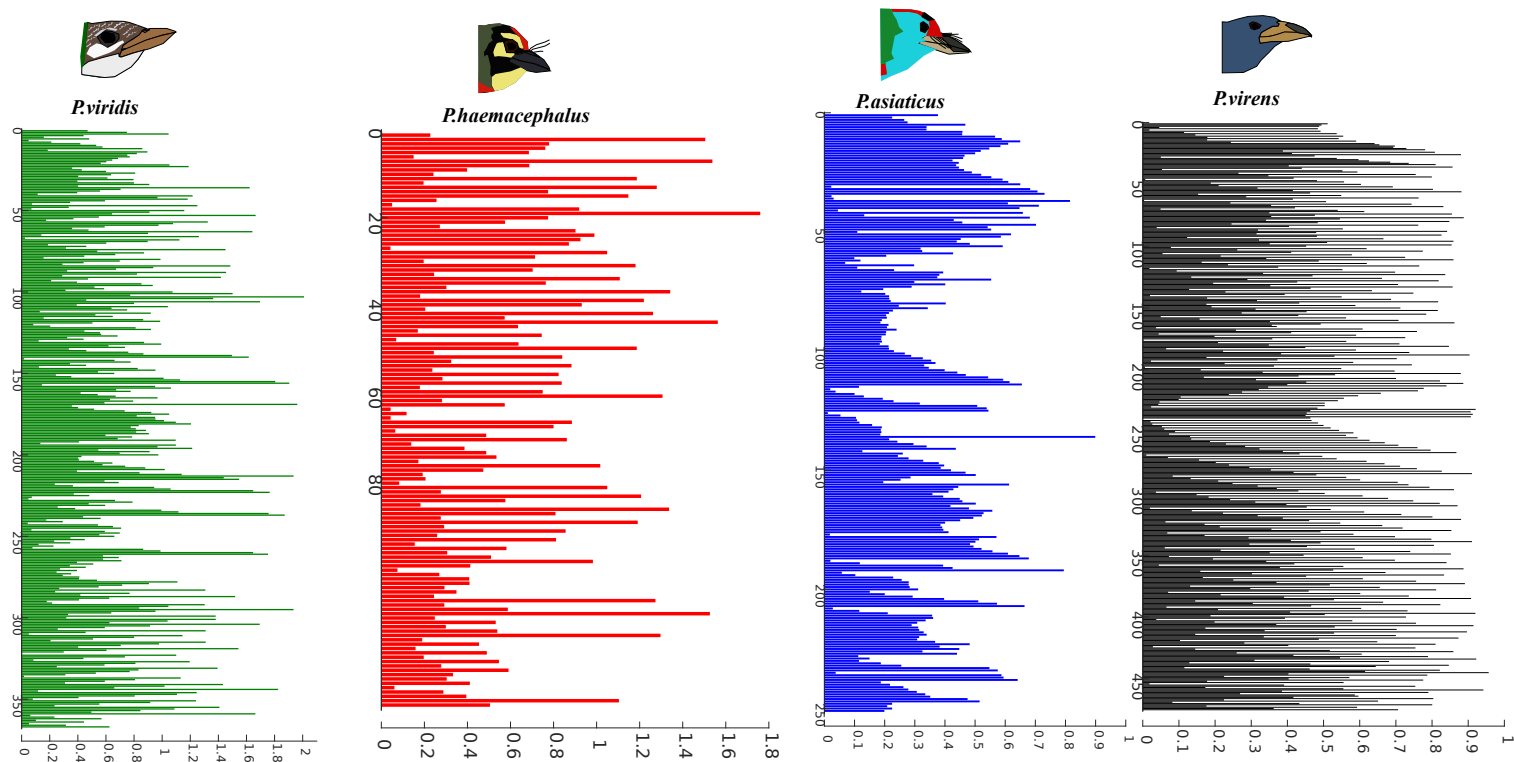


Western Himalayas

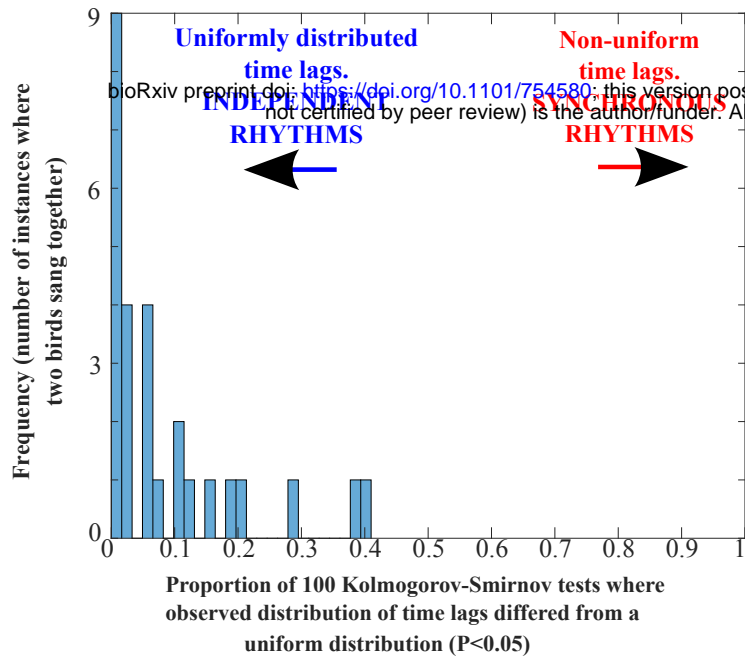


B



A**B**

**Time lag between simultaneously
vocalizing individuals (s)**

A**N=27****B****N=108**