Simultaneously vocalizing Asian barbets adopt different frequencies without coordinating temporal rhythms

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Abstract

Sound stream segregation is an important challenge faced by simultaneously vocalizing animals. In duetting passerine birds, coordinating vocal timing helps minimize overlap. Alternatively, in birds that do not coordinate their vocalizations, sound stream segregation may involve other mechanisms. For example, birds are known to use frequency differences to segregate sound streams, and vocalizing at different frequencies may enable them to remain distinct from each other. Here, I present data showing that conspecific individuals of four species of Asian barbets vocalize at distinctly different peak frequencies from each other. Additionally, they also differ in repetition rate such that each species exhibits two peaks in frequency-repetition rate space. However, conspecific individuals across species do not temporally coordinate with each other during vocal interactions, maintaining independent and highly stereotyped individual rhythms together with different peak frequencies. Frequency differences between individuals may facilitate sound stream segregation when calls overlap in time. I hypothesize that simple, uncoordinated temporal rhythms with different frequencies may have given rise to the more complex coordination seen in duetting birds.

Introduction

Animal choruses represent a striking natural example of the 'cocktail party problem', where individuals must segregate relevant information from competing streams of sound[1,2]. Vocalizing at differing frequencies[3], or altering vocal timing[4,5] may minimize masking interference from overlapping sounds. Many bird species sing complex duets, which serve to communicate or cooperatively defend territories[6,7]. Duetting pairs coordinate vocal timing, resulting in a definite phase relationship between simultaneously vocalizing birds[8,9]. Other 'duetters' simply sing together without coordination, and their vocalizations drift in and out of phase with each other[6,10]. As a result, simultaneously vocalizing conspecifics may overlap in time. The mechanisms employed by these birds to remain distinct are relatively poorly understood.

Here, I study the vocal strategies of four species of Asian barbet (Piciformes: Megalaimidae)[11] in two regions of India. Each region possesses two species with different vocal frequencies from each other[12]. I examined whether simultaneously vocalizing conspecific barbets also exhibited frequency differences, as well as whether they coordinate vocal timing to minimize temporal overlap. Understanding the vocal strategies employed by these non-passerine birds has implications in understanding the evolution of coordinated signals such as pair-displays.

Materials and Methods

Recording

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

Analysis

Using Raven Pro 1.5 (Cornell Laboratory of Ornithology, Ithaca, NY, USA), I digitized vocalizations of barbets from each recording (Hann window size 512 samples with overlap of 256 samples) and calculated peak frequencies (PF) as well as the inter-phrase interval (IPI, the time gap between the end of one phrase and the beginning of the next). For each species, I digitized approximately 2500 individual phrases (1-5 notes/phrase depending on the species). I listened to all recordings using headphones while labeling vocalizations, differentiating conspecific individuals by the differences in relative amplitude (birds that were further from the microphone were softer in recordings, and distinguishable in Raven). I measured the interquartile range or IQR of IPI (for 108 total instances of a vocal barbet), to quantify stereotypy. Secondly, to examine whether simultaneously vocalizing conspecifics (36 instances) were temporally synchronous or asynchronous with each other, I calculated the time lag between the beginning of each phrase of one individual and the closest call of the other using MATLAB (Mathworks Inc., Natick, MA, USA). If birds were synchronous, I predicted that the distribution of time lags across a bout should show a clear peak and low coefficient of variation (i.e. a stereotypical time lag between individuals)[13]. However, an asynchronous bout would imply independent rhythms from each other; the two individuals would thus drift in and out of phase, resulting in a uniform distribution of time lags. For each instance with 5 or more measured time lags (27/36), I performed two-sample Kolmogorov-Smirnov tests against 100 randomly generated uniform distributions spanning the same range of values. I scored the results as 0 if they did not differ significantly from uniform ($P>0.05$), or 1 if they did ($P<0.05$), and measured the percentage of total 1's (out of 100 tests) for each of the 27 instances. A score of 0 indicated a uniform distribution of time lags consistent with independent temporal rhythms, and a score of 1 indicated a constant time lag consistent with two birds singing in coordination.

Results

Conspecific barbets sing at different frequencies and repetition rates

PF-IPI probability density plots reveal bimodal distributions for each species, indicating intraspecific variation in PF and IPI (Figure 1B, see supplementary videos for 3D rotations). This is most pronounced in *P. haemacephalus*, suggesting two distinct types of song, a faster song at 0.7KHz, and a slower song at about 0.95KHz. Both *P.viridis* and *P.virens* exhibit two peaks in PF-IPI space, also indicating faster and slower songs. *P.asiaticus* also exhibits a bimodal probability density distribution, but the two peaks in my dataset indicate smaller differences in IPI than the other species.

Simultaneously vocalizing conspecifics sing at independent rhythms without synchronization

Across 36 instances of simultaneously vocalizing conspecifics (pooled data from all 4 species), I consistently observed differences in frequency and repetition rate between conspecific individuals (spectrograms in Figure 2A). A probability density plot of the differences between two individuals exhibited a non-zero peak in both PF and IPI (Supplementary Figure 1A). Conspecifics thus vocalize at different frequencies and repetition rates from each other.

I next sought to establish whether vocally interacting conspecific barbets adjusted their repetition rates to maintain synchrony with their vocal neighbors. The time lags between the calls of two individuals have very high coefficients of variation for each species (*P.haemacephalus:* 144.13%, *P.viridis:* 164.52%, *P.virens:* 182.55%, *P.asiaticus:* 197.11%), supporting a lack of vocal timing coordination[6]. Time lags exhibit a range of values across all 4 species, as opposed to a single value that would be expected if two individuals coordinated vocal timing by phase-locking (Figure 2B). When compared to 100 randomized uniform distributions (27 instances, see Methods), time lags fit a uniform distribution 92% of the time on average (average score 0.08, P>0.05, Supplementary Data, Supplementary Figure 1B, also see Methods). This uniform distribution of time lags, together with high CVs, thus supports barbets vocalizing with independent temporal rhythms rather than synchronizing with each other. Further, each barbet maintains its individual rhythm even when vocalizing with conspecifics. The probability density plot of IQRs for the IPI of each individual barbet peaked at 47ms (Supplementary Figure 1C), indicating <50ms jitter in vocal timing across all species (including measurement-related variation). This analysis included every individual instance of a vocal barbet across the dataset (solo and with other conspecifics), in spite of which I still observed a sharp peak indicating a precise vocal rhythm. This further supports the idea that barbets maintain stable, independent vocal rhythms regardless of whether they vocalize solo or with conspecifics.

Discussion

Avian duets and other vocal interactions have received much study for the precisely coordinated vocal timing between individuals[6,9]. However, some ‘duetters’ exhibit independent rhythms with no phase-locking or coordination between simultaneously vocalizing individuals[6]. My data suggests that Asian barbets fall into this latter category, and I also find that simultaneously vocalizing individuals tend to differ in the peak frequencies of their vocalizations. If two barbets vocalize at independent and different rhythms, their calls will drift in and out of phase with each other (resulting in a uniform distribution of time lags between the two individuals, as opposed to the single peak one might expect if they were coordinated with each other). It is noteworthy that two of the species I studied (*P.haemacephalus* and *P.virens*) have been described in the literature as duetters[6]. However, all four species studied here exhibit similar patterns of frequency and repetition rate differences between individuals, without timing coordination. This indicates that all Asian barbets may vocalize with independent, uncoordinated rhythms.

Dilger[14] described 'duetting' in *P.haemacephalus* involving members of a pair singing at different frequencies. Across species, I find that some individuals sing together with large PF and IPI differences, and others with relatively small PF and IPI differences. However, none of these cases exhibit evidence of a 'call-answer' type of vocal coordination as seen in duetting passerine birds. Instead, barbets appear to simply adopt different temporal rhythms from each other, which may involve paying attention only to the start of another bird's bout. Although different repetition rates may reduce temporal overlap to some extent, some vocalizations of two individuals will still overlap in time. In this case, frequency differences between individuals may support sound stream segregation[3,15]. Sympatric heterospecific barbets occupy distinct frequency bands[12], and my data therefore suggests that smaller frequency differences may also enable segregation of conspecifics within each species' band.

Some species of the related African barbets (Lybiidae:*Trachyphonus*) appear to exhibit coordination between duetting individuals[8,16], although other species may exhibit independent rhythms[10]. It is possible that barbets may sometimes coordinate their rhythms over short time scales, although my study does not find evidence of this. The similarly non-passerine pheasant-coucal also exhibits pair-singing, with each partner vocalizing at a different frequency[17]. Passerine birds may have evolved temporally coordinated duets multiple times[6,13,18], and it is possible that these may have arisen from uncoordinated simultaneous singing such as that seen in non-passerines. Comparative study of vocal strategies may help understand the ancestry of complex, temporally coordinated duets.

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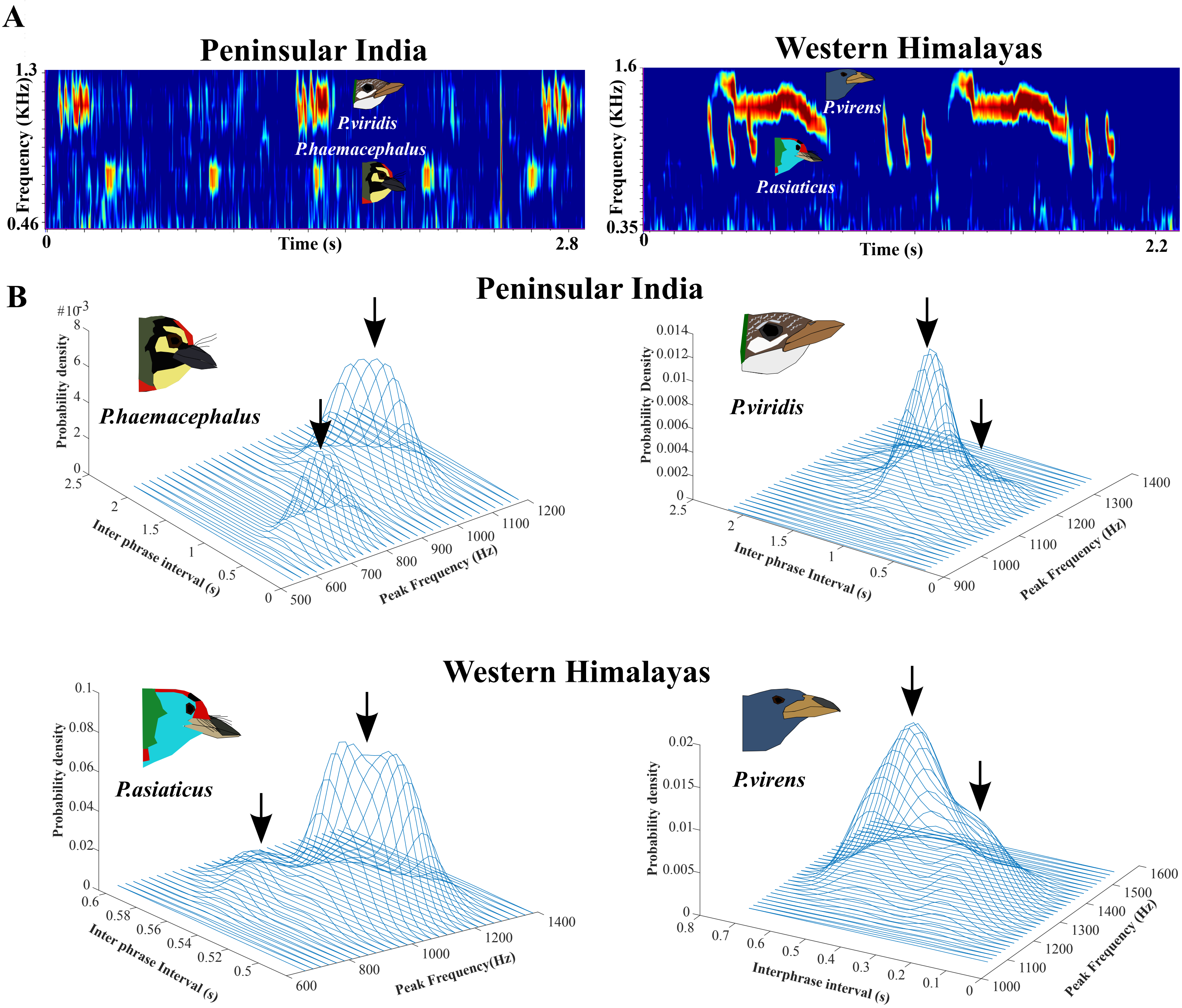
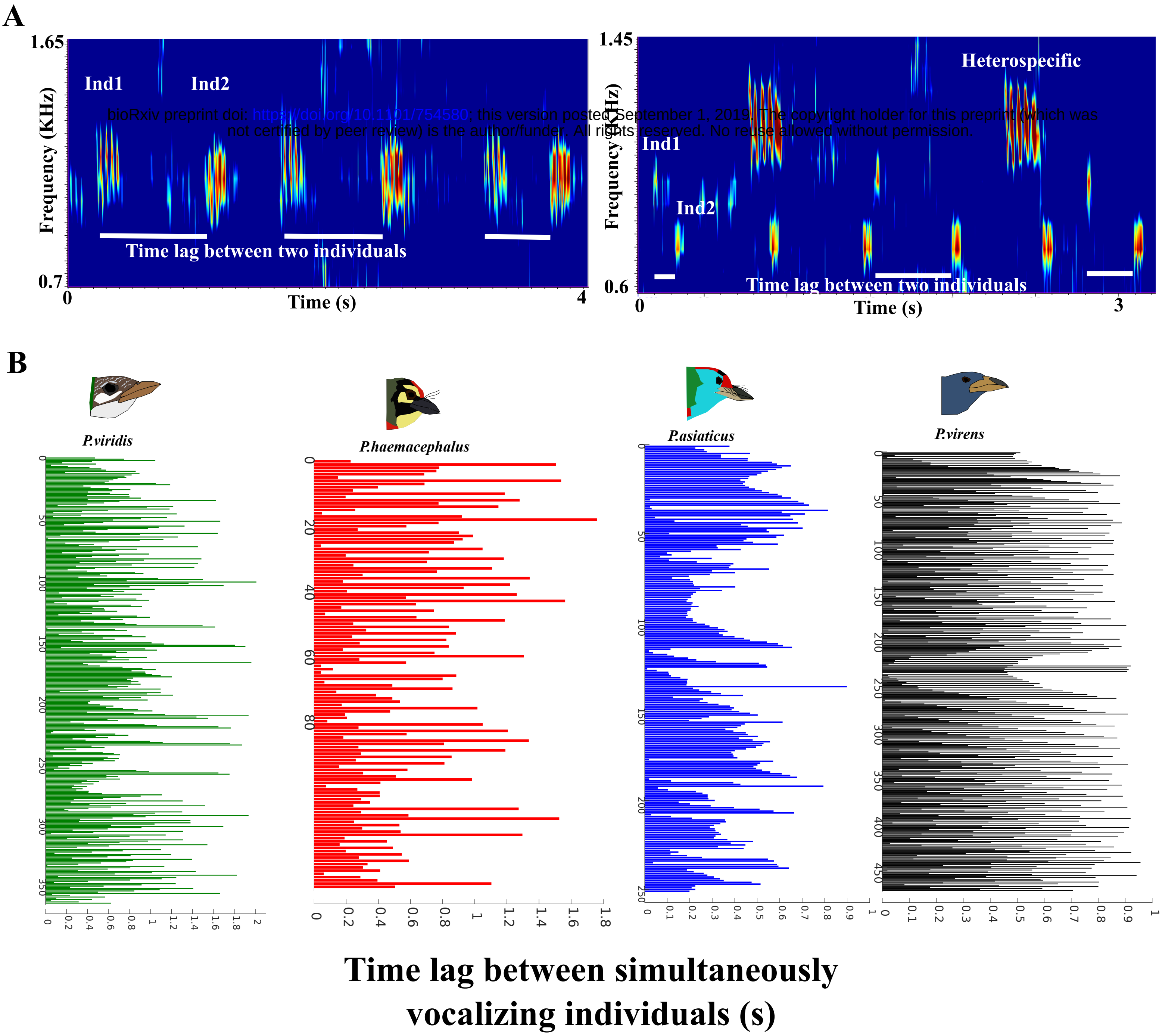
Figure legends

Figure 1: A. Spectrograms of barbet vocalizations from Peninsular India (left) and the Western Himalayas (right). **B.** Three-dimensional probability density distributions indicating the occurrence of different PF and repetition rates (IPI) for each species. For each instance of a vocalizing barbet in the dataset, these plots contain the mean plus and minus one SD for PF, and median, upper and lower quartile values for IPI, to represent the overall variation (both inter- and intra-individual) in frequency-time space. This last is for illustrative purposes only, and the quartiles have otherwise only been used to calculate the IQR for the IPI of each species.

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

Supplementary Figure 1: A. 3D probability density distribution for inter-individual differences in PF and IPI. The peak suggests that most simultaneously vocalizing individuals have about a 100Hz difference in PF and a 300-500ms difference in IPI. **B.** Proportion of 100 Kolmogorov-Smirnov tests in which the observed distribution of time lags differed from a random uniform distribution (for 27 instances of two conspecific barbets vocalizing together). In 18/27 cases, the observed distribution fit >90% to a uniform distribution (x-axis values <0.1, indicating independent temporal rhythms without synchrony). Almost all other instances also fit well to a uniform distribution (the lowest being a 59% fit to uniform, x-axis value 0.41), again supporting independent vocal rhythms. **C.** Distribution of IQRs for the IPI of each individual instance of a vocalizing barbet across the entire dataset (both solo and simultaneous calling, N=108). The peak at 47ms indicates very low IQRs, and therefore a highly stereotyped temporal rhythm regardless of whether the barbet is vocalizing solo or with conspecifics.


A
Peninsular India
1.3
Frequency (KHz)
0.46
0
Time (s)
2.8
P.viridis
P.haemacephalus
Western Himalayas
1.6
Frequency (KHz)
0.35
0
Time (s)
2.2
P.virens
P.asiaticus
B
Peninsular India
P.haemacephalus
Probability density
Inter phrase interval (s)
Peak Frequency (Hz)
P.viridis
Probability Density
Inter phrase Interval (s)
Peak Frequency (Hz)
Western Himalayas
P.asiaticus
Probability density
Inter phrase Interval (s)
Peak Frequency(Hz)
P.virens
Probability density
Interphrase interval (s)
Peak Frequency (Hz)


A
1.65
0.7
Frequency (KHz)
Ind1
Ind2
Time lag between two individuals
0
4
Time (s)
1.45
0.6
Heterospecific
Ind1
Ind2
Time lag between two individuals
0
3
Time (s)
B
P.viridis
P.haemacephalus
P.asiaticus
P.virens
Time lag between simultaneously vocalizing individuals (s)