

# An analysis of Greater Flameback *Chrysocolaptes guttacristatus* vocalisations and their taxonomic and biogeographic implications

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**Abstract:** The Greater Flameback *Chrysocolaptes guttacristatus* is a woodland species that is distributed in the humid forests of the Oriental Region. We analysed the contact calls, flight calls, and drumrolls of three taxa—*C. guttacristatus socialis* of the Western Ghats, *C. stricklandi* of Sri Lanka, and *C. guttacristatus sensu stricto* of the Himalayas and South-east Asia. We found that *socialis* had markedly different contact and flight calls compared to *guttacristatus sensu stricto*; in some respects more marked than those of *stricklandi* to *guttacristatus*. A preliminary analysis of available drumrolls also indicated *socialis* to be very distinct. This divergence in vocalisation coupled with already well-known modest differences in plumage and morphometrics suggests a distinct lineage that argues for a species status for *socialis* as ‘Malabar Flameback’.

The Greater Flameback *Chrysocolaptes guttacristatus* ranges from the Western Ghats to south-eastern China and certain Sunda Islands including Borneo, Sumatra and Java (del Hoyo et al. 2020). The species, formerly, was part of a larger complex under *C. lucidus* (Dickinson & Remsen 2013) that included six subspecies in the Philippines, one each in Java, the Kangean Islands, and Sri Lanka. Based on the Winkler et al. (2014) molecular phylogeny of this complex, most contemporary taxonomies (Clements et al. 2019: HBW & BirdLife International 2020; Gill et al. 2021) restrict the Greater Flameback to three to four subspecies: the widespread nominate, *guttacristatus* from north-western India along the Himalaya, through Vietnam/China (west Himalayan *sultaneus* is usually not recognised); *socialis* in the Western Ghats; *indomalayicus* in the Malay Peninsula, Sumatra, and Java (excluding the eastern region); and the disjunct *andrewsi* in north-eastern Borneo. The remaining taxa of this complex have been assigned to different species: the Crimson-backed Flameback *C. stricklandi* in Sri Lanka; Javan Flameback *C. strictus* in eastern Java and the Kangean Islands; and four strikingly different species in the Philippines (Buff-spotted Flameback *C. lucidus*, Luzon Flameback *C. haematribon*, Red-headed Flameback *C. erythrocephalus*, and Yellow-faced Flameback *C. xanthocephalus*). Rasmussen & Anderton (2012), additionally, accorded specific status to the Western Ghats *socialis* as the Malabar Flameback based on size, voice, and minor differences in plumage; but this is not recognised by any other global taxonomy and del Hoyo et al. (2020) recommended further study. In this note, we accessed online audio databases for a more comprehensive analysis of the different vocalisations of *socialis*, in relation to nominate *guttacristatus* and also the Crimson-backed Flameback, which is, geographically, the nearest member of *socialis* in this superspecies.

## Methods

We used all available calls of the Greater Flameback from the websites—[www.xeno-canto.org](http://www.xeno-canto.org), <https://avocet.integrativebiology.natsci.msu.edu/>, and [www.macaulaylibrary.org](http://www.macaulaylibrary.org)—as well as those obtained from certain private collections. As per Rasmussen & Anderton (2012), Flamebacks utter two types of calls—a regular call that we designate here as the ‘contact call’ and another ‘flight call’. In addition, all woodpeckers have a drumroll that is created by tapping a substrate. We classified our dataset into three sets by ear: (a) Contact call, (b) Flight call, and (c) Drumroll. To avoid any particular recording from influencing the analysis, we selected one vocalisation within each recording that we marked as ‘high’ or ‘medium’ quality based on the impact of background noise on the recording. We eliminated a few calls where the identification of the species was suspect. Thus we had a large set of recordings classified in **Table 1**. However, we were particularly handicapped in certain cases, due to the paucity of recordings.

- i. We had no good recordings from the Eastern Ghats or east-central India that could be analysed along with other recordings. The two available recordings, one each from central Eastern Ghats and east-central India had to be aurally assigned as they were faint and hard to pick comparable measurements that can be used for analysis.
- ii. We had no recordings of *andrewsi* from Borneo, and just two contact call recordings of *indomalayicus* and hence they were analysed along with *guttacristatus sensu stricto*
- iii. We had no flight calls of Crimson-backed Flameback
- iv. Number of samples of drumroll calls were very few across the range.

**Table 1.** Number of samples for each taxon and each sound type

|                                       | Contact calls | Flight calls | Drumrolls |
|---------------------------------------|---------------|--------------|-----------|
| <i>C. socialis</i>                    | 33            | 8            | 4         |
| <i>C. guttacristatus</i> <sup>1</sup> | 58            | 16           | 6         |
| <i>C. stricklandi</i>                 | 10            | –            | 4         |

<sup>1</sup>We had two recordings of *C. g. indomalayicus* that are included under *guttacristatus*. No recordings of *C. g. andrewsi* were available.

We analysed the sounds with the software Raven Lite (<https://ravensoundsoftware.com/software/raven-lite/>) with a spectrogram window size of 512 with brightness and contrast set appropriately to obtain the sharpest sonograms. A single observer (AC) manually observed and measured several sonogram parameters (Table 2; Figs. 1, 7, 10). We used the second harmonic consistently for all measurements, as the first harmonic was sometimes faint in some sonograms. The number of notes/second was calculated by counting the number of distinct notes for a duration of half-a-second starting with the first note and doubling the value. We opted for a different note selection in Contact and Flight calls: Contact calls are delivered when the bird–observer distance is nearly static, while flight calls are those that are heard as the bird is approaching, or moving away from, the observer, and hence, the first note is not always recorded or not of sufficient quality. Therefore, we used the loudest note for our analysis of Flight calls.

We did a Principal Component Analysis (PCA) on Contact and Flight calls to identify possible clusters using ‘prcomp’ function in the R Stats Package (<https://stat.ethz.ch/R-manual/R-devel/library/stats/html/OOIndex.html>) and verified the results by listening to the recordings. As we had multiple response variables, we conducted pair-wise PERMANOVA (Anderson 2017) following Martinez (2020) built on the adonis function from vegan package in R, with permutations set to 10000 and method set to bray, over both Contact calls and Flight calls for hypothesis testing of significance. For Drumrolls, we conducted the ANOVA, followed by Tukey tests.

Aural analysis of Greater Flameback Contact calls indicated individual note-level variations between the taxa in the maximum

**Table 2.** Parameters used for different type of vocalisations (P: used for PCA, S: Used to illustrate the series, B: Used only for box plots)

| No | Parameters                            | Contact calls | Flight calls | Drumrolls |
|----|---------------------------------------|---------------|--------------|-----------|
| 1  | Number of notes/sec                   | P             | P            | B         |
| 2  | Duration of the first note            | P             | -            | -         |
| 3  | Duration of the loudest note          | -             | P            | -         |
| 4  | Time interval between first two notes | P             | P            | -         |
| 5  | Maximum frequency of the first note   | P             | -            | -         |
| 6  | Maximum frequency of the loudest note | -             | P            | -         |
| 7  | Minimum frequency of the first note   | P             | -            | -         |
| 8  | Minimum frequency of the loudest note | -             | P            | -         |
| 9  | Bandwidth of the first note           | P             | -            | -         |
| 10 | Bandwidth of the loudest note         | -             | P            | -         |
| 11 | Maximum frequency of each note        | S             | -            | -         |
| 12 | Time interval between each note       | S             | -            | S         |

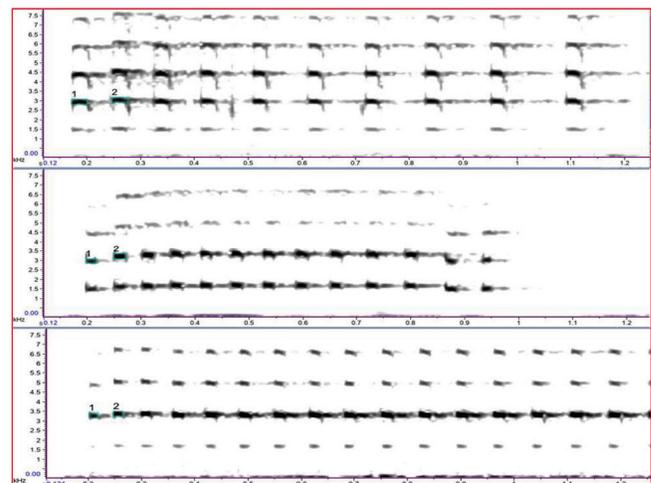
frequency and inter-note intervals. Including individual note level parameters in the PCA did not change the results, but we created time/frequency series using contact calls that had long duration (minimum 12 notes, 31 samples in total) measuring both maximum frequency of each note, and inter-note interval between every note till the end of the call, to illustrate this point better.

## Results

We use GC (*C. guttacristatus*), SO (*C. socialis*) and ST (*C. stricklandi*) as acronyms while discussing the results.

### Contact calls

We found that SO is vocally very distinct from GC as borne out by the contact call sonograms (Fig. 1). The majority of SO Contact calls can be unanimously assigned to this taxon by checking the number of notes per second (14–22/s vs 6–12/s in GC, and 12–16/s in ST (see Table 3; Fig. 3a). Interestingly, ST was found to be intermediate between SO and GC groups in PCA, ST being closer to SO (Fig. 2). The first two principal components explained 76% of the variation with PC1, explaining 51.85 % of total variation (loading on number of notes/second), and PC2 explaining 24.36% of total variation (loading on the minimum and maximum frequency of the first note). PERMANOVA over all six parameters gave a significance of  $p < 0.05$  for GC vs SO ( $F=21.96$ ,  $Df = 1$ ,  $p = 0.0001$ ) and GC vs ST ( $F= 9.31$ ,  $Df = 1$ ,  $p=0.0038$ ) while the results were not significant for SO vs ST. GC has a slightly longer duration of the first note on an average (Table 3; Fig. 3d) than both SO and ST, but there is much overlap. Both SO & ST have a slightly higher median frequency than GC (Figs. 3e, 3f). GC notes are more spaced out (Fig. 3c) than both SO and ST though there is some overlap at the extremes (Table 3). This is borne out by Fig 4a., where the inter-note interval kept increasing for GC while it does not for SO. Interestingly, the inter-note intervals increase even more strongly in ST than GC, starting with inter-note intervals that are alike SO but ending more in the band of GC. The maximum frequency of the notes (Fig. 4b), for all taxa, shows minor fluctuations but does not appreciably differ in its variance—but GC has a lower frequency than both other taxa. However, our limited samples of ST do indicate a slight rise in the maximum frequency compared to both SO and GC.



Figs. 1a–1c. Contact calls: From top: *C. guttacristatus* (ML183026), *C. socialis* (ML338859301), and *C. stricklandi* (ML178535). Recordists: Roger McNeill, Esha Munshi, and Roger McNeill respectively

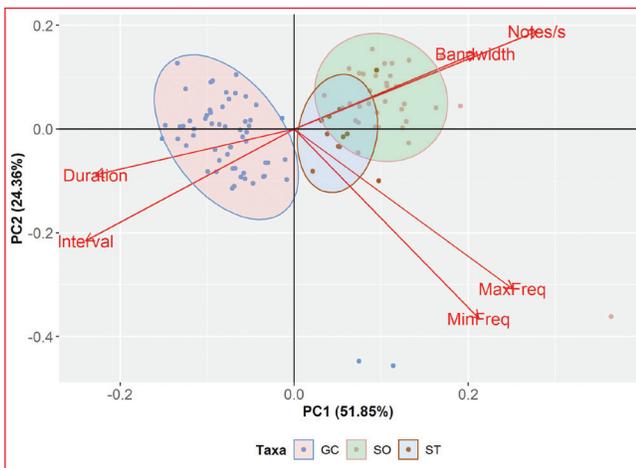
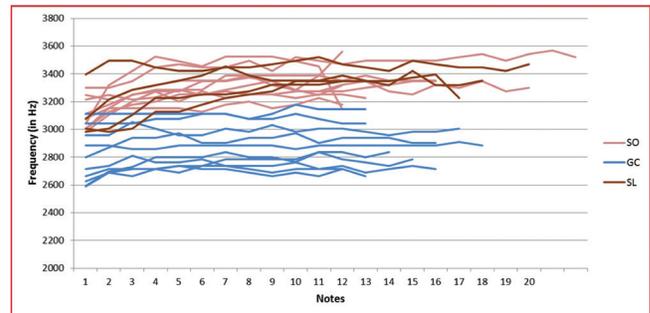
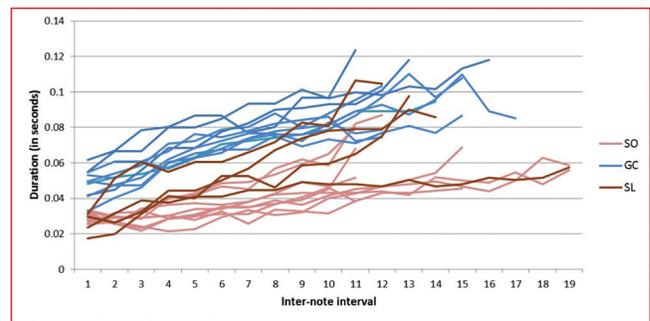
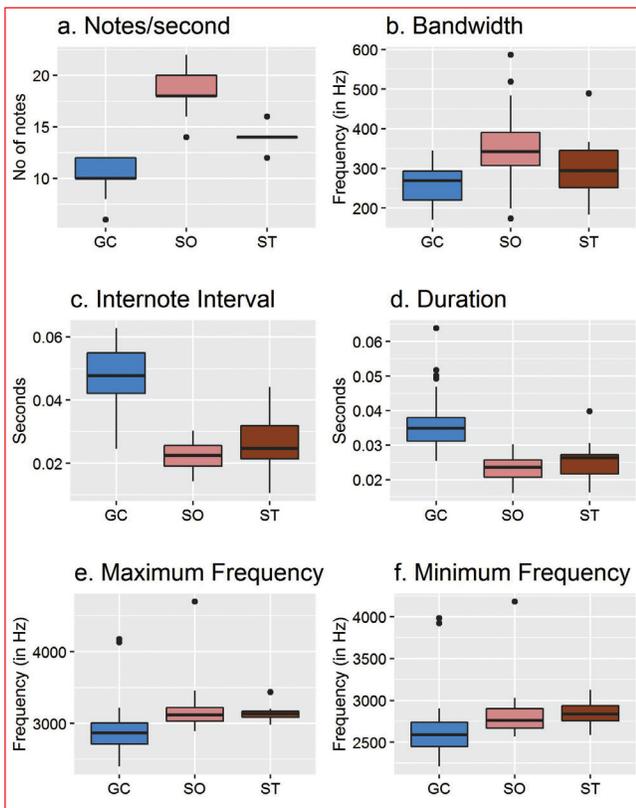


Fig 2. PCA of Contact calls showing *C. socialis* clustering differently from *C. guttacristatus* group with *C. stricklandi* being intermediate. PC1 loaded 0.47 of number of notes/s and PC2 loaded on the minimum (-0.62) and maximum (-0.52) frequency of the first note.



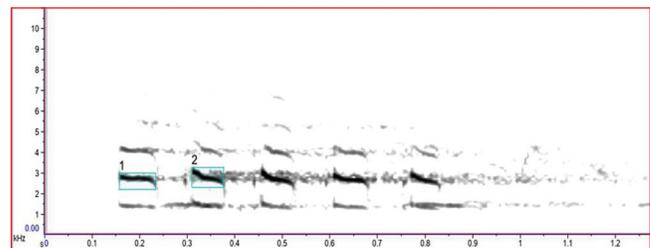
Figs. 4a–4b. Time and frequency series showing duration of inter-note intervals, and maximum frequencies for each note in the Contact calls of three taxa.



Figs. 3a–3f. Box plots of call parameters of the Contact call for the three taxa.

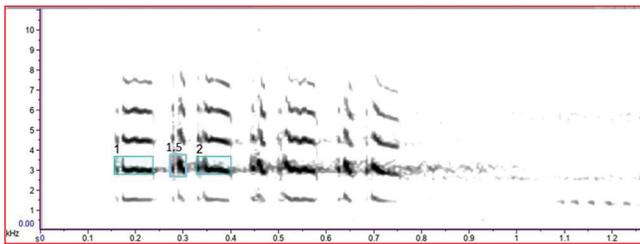
### Flight calls

We found that the Flight calls of SO can be clearly separated from GC by the presence of what we call 'note 1.5', a short half note between the first and second notes, which is absent in every GC Flight call (see Figs. 5a, 5b). There are no samples of ST Flight calls to verify this characteristic. However, PCA clearly segregated GC and SO on Flight calls (Figs. 6, 7a–7f; Table 4). The first two principal components explained 72% of the variation with PC1 loading on notes/s, minimum frequency and interval after the loudest note, while PC2 loading on bandwidth, maximum frequency and duration of the loudest note. PERMANOVA over all six parameters gave a significance of  $p < 0.05$  ( $F = 14.32$  Df = 1,  $p = 0.00099$ ).



| Table 3. Vocalisation parameters with median and range for contact calls. PERMANOVA provided a significance of $p < 0.05$ for GC vs SO and GC vs. ST |                                   |           |   |             |                            |             |                             |       |
|--|-----------------------------------|-----------|---|-------------|----------------------------|-------------|-----------------------------|-------|
| Taxa   | Maximum frequency of note 1 (Hz.) |           | Time interval between first two notes (s) |             | Duration of first note (s) |             | Number of notes per seconds |       |
|  | Median                            | Range     | Median                                    | Range       | Median                     | Range       | Median                      | Range |
| <i>C. guttacristatus</i>   | 2868                              | 2402–4179 | 0.048                                     | 0.025–0.063 | 0.035                      | 0.025–0.064 | 10                          | 6–12  |
| <i>C. socialis</i>   | 3117                              | 2894–4700 | 0.022                                     | 0.014–0.030 | 0.023                      | 0.016–0.030 | 18                          | 14–22 |
| <i>C. stricklandi</i>  | 3136                              | 2981–3439 | 0.025                                     | 0.011–0.044 | 0.026                      | 0.016–0.040 | 14                          | 12–16 |

| Table 4. Vocalisation parameters with median and range for Flight calls. PERMANOVA provided a significance of $p < 0.05$ |   |             |   |               |                              |               |
|--|---|-------------|---|---------------|------------------------------|---------------|
| Taxa   | Maximum frequency of loudest note (Hz.) |             | Time interval between first two loudest notes (s) |               | Duration of loudest note (s) |               |
|  | Median                                  | Range       | Median  | Range         | Median                       | Range         |
| <i>C. guttacristatus</i>   | 3041                                    | 2786 - 3963 | 0.057   | 0.044 - 0.084 | 0.075                        | 0.033 - 0.099 |
| <i>C. socialis</i>   | 3518                                    | 3055 - 3802 | 0.092   | 0.085 - 0.117 | 0.085                        | 0.071 - 0.105 |



Figs. 5a–5b. Flight calls: From top *C. guttacristatus* (ML284829) and *C. socialis* (ML283090). See note 1.5 that is present in *C. socialis* but not in *C. guttacristatus*. Recordist: Both calls: Peter Boesman

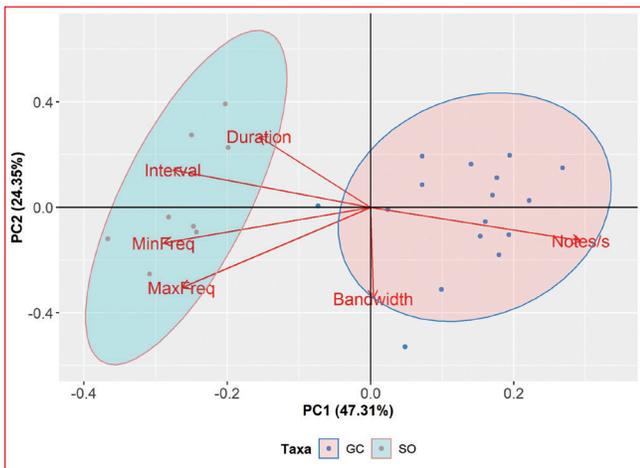
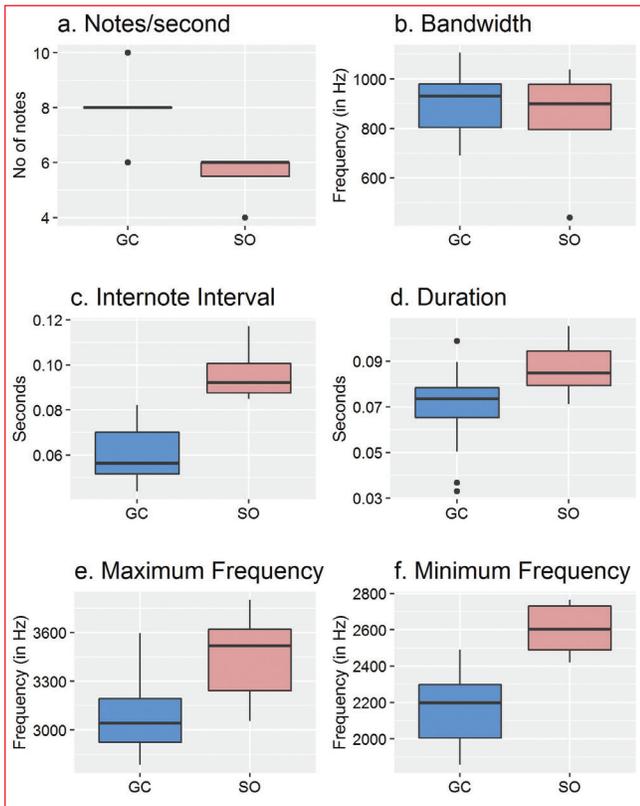


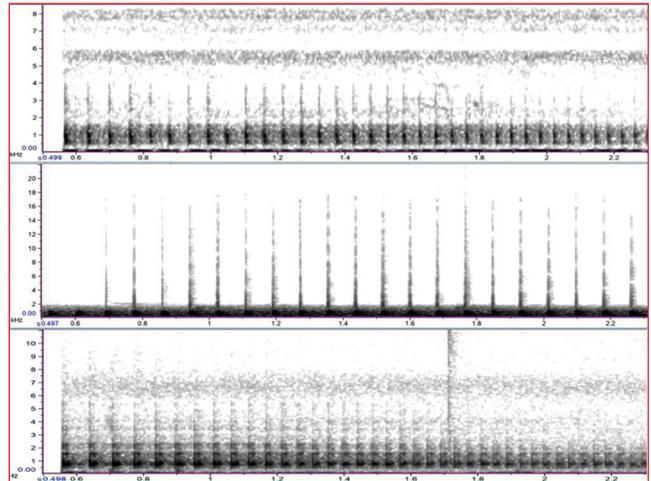
Fig. 6. PCA of Flight calls showing *C. socialis* clustering differently from *C. guttacristatus* group. PC1 loaded 0.50 on Notes/s (-0.50 on minimum frequency of loudest note, -0.47 on interval after loudest note) and PC2 loaded -0.59 on the bandwidth (-0.52 on maximum frequency of the loudest and 0.46 on duration of the loudest note).



Figs. 7a–7f. Box plot of call parameters of the Flight call of the three taxa.

### Drumroll

Based on the limited number of samples, Drumrolls of SO had a steady inter-tap interval compared to GC and ST (Table 5; Figs. 8a–8c, 9). Our limited samples of GC and ST indicate that their inter-tap interval reduces (Fig. 10) through the Drumroll from 0.06-0.09s to 0.03-0.05s. More samples are required to establish the same.



Figs. 8a–8c. Drumming (part of a full drumroll): From top *C. guttacristatus* (ML165179), *C. socialis* (ML163865751) and *C. stricklandi* (XC453473). Recordists: Martjan Lammertink, Pradnyavant Mane, and Oscar Campbell respectively.

Table 5. Median and range of number of taps/s of Drumroll. ANOVA with Tukey test gave 95% significant differences for *C. guttacristatus*–*C. socialis* ( $p = 0.0000059$ ) and *C. stricklandi*–*C. socialis* ( $p = 0.0000033$ ) pairs only

| Subspecies               | Number of taps/sec |       |                             |
|--------------------------|--------------------|-------|-----------------------------|
|                          | Median             | Range | Rasmussen & Anderton (2012) |
| <i>C. guttacristatus</i> | 18                 | 16–20 | 16–20                       |
| <i>C. socialis</i>       | 13                 | 12–18 | 15                          |
| <i>C. stricklandi</i>    | 20                 | 17–21 | 25                          |

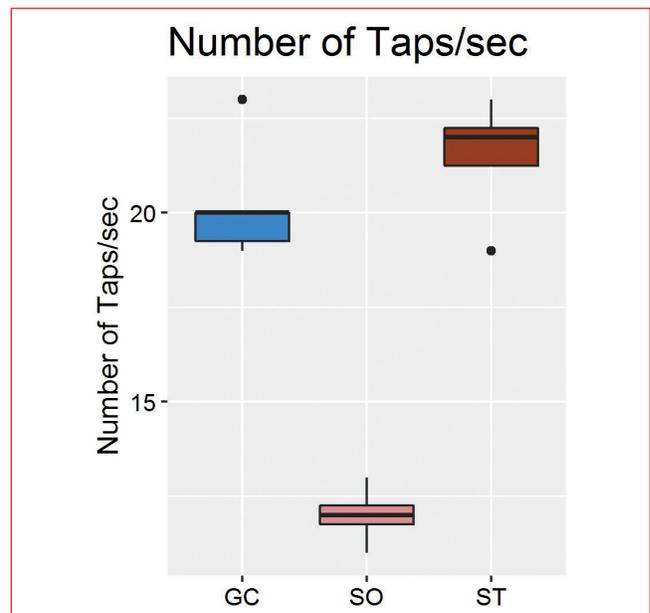


Fig. 9. Box plot for 'Number of taps/second' for the Drumrolls of three taxa.

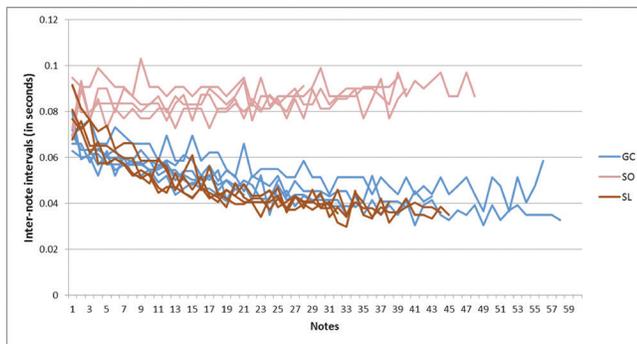


Fig. 10. Time series showing duration of inter-tap intervals for the Drumrolls of three taxa.

## Discussion

Rasmussen & Anderton (2012) have documented that SO has strikingly different contact calls from GC; which they described as ‘much faster, irregular, relatively weak, short, tinny, chattering musical incomplete-sounding rattles that often rise or waver in pitch greatly, and may decelerate slightly’. Similarly, the ST contact calls have been described as ‘very rapid, slightly decelerating, evenly rising short trills, the notes distinct, shrill and sharp. Stronger and much more even than Malabar, and much more faster than Greater’. Our quantitative analysis (Table 6) supports the initial findings by Rasmussen & Anderton (2012) that SO and ST are vocally distinct from GC in their contact calls. The speed of delivery (notes/s), spacing of notes (inter-note interval), duration of the note, rate of deceleration (increasing inter-note intervals) and the pitch (frequency) of the notes came out as the discerning factors. Other descriptive terms are hard to measure on sonograms as they either depend on the distance of the bird from the observer (e.g. weak vs strong that depends on relative energy, number of harmonics) or the actual variance (irregular, waver) and, hence, we cannot comment on those aspects from our study. There is no literature on the difference in Flight calls between the three species. However, we found that there is a consistent difference between the Flight calls of SO and GC and all calls can be unanimously assigned by the presence of *note 1.5* in SO (Fig. 5a–5b). Though Drumroll of all taxa has been described in Rasmussen & Anderton (2012), they did not emphasise any specific differences. With a limited number of samples, we showed that the drumroll of SO is slower (higher inter-tap interval) and even (inter-tap interval not

changing) compared to both GC and ST, where their drumrolls accelerates (inter-tap interval reduces). However, drumrolls in woodpeckers are known to have a gender bias (Budka et al. 2018) and hence a more focussed study, with each recording marked to a particular sex, would be needed to handle these variations. We also did not analyse the frequency or energy of the Drumroll, as they are dependent on extraneous factors like the nature of the substrate, distance of the recorder or, even, the propensity of the foliage to reflect sounds. However, studies have found that a woodpecker’s drumming signal has not been selected for maximising information for species identity in the signal itself though it has preserved the efficacy of its species’ signature (Garcia et al. 2020). We did not conduct playback experiments, but Rasmussen & Anderton (2012) indicate that a playback experiment with GC calls in Goa did not evoke a response from SO, without providing further details. Playback of Drumrolls and noting their responses would certainly provide additional information on species divergences.

All three species are allopatric. However, SO and GC distributions come close in Andhra Pradesh. GC occurs in Papikonda Wildlife Sanctuary (17.33°N, 81.29°E) along the Godavari River, while SO is found in the Nallamala Hills (16.06°N, 78.95°E); they are separated by the ~300 km wide plains between the Krishna and Godavari rivers, an ancient biogeographical barrier for species’ dispersal (Ramachandran et al. 2016). We did not get any good recordings from Andhra Pradesh, but a weak recording of a Contact call from the northern end of the Nallamala Hills (at 16.18°N, 78.64°E) was clearly that of a SO, with no intermediate characteristics. Similarly, a contact call recording in Chhattisgarh (at 18.93°N, 82.03°E) in east-central India can unanimously be assigned to GC. We have other gaps in our sample size that are described in the methodology but we present strong evidence that SO differs from GC in all known vocalisations, more so than ST, which has been already accorded species status.

Sometimes the avifauna of the Western Ghats and Sri Lanka share similarities when compared to that of the Himalaya (e.g. Legge’s/Mountain Hawk Eagle *Nisaetus kelaarti/nipalensis*, Sri Lanka/Hodgson’s Frogmouth *Batrachostomus moniliger/hodgsoni*); while in other cases, Sri Lanka is dissimilar to both, the Western Ghats and the Himalayas (e.g. Vernal/Sri Lanka Hanging Parrot *Loriculus vernalis/beryllinus*). From acoustic analysis, it appears that both the Western Ghats (SO) and Sri Lanka (ST)

**Table 6.** Qualitative summary of the differences in vocalisation

| Vocal character                           | <i>C. guttacristatus</i> | <i>C. stricklandi</i> | <i>C. socialis</i>     |
|---|--------------------------|-----------------------|------------------------|
| Contact call (Speed of Delivery)          | Slower                   | Intermediate speed    | Fastest                |
| Contact call (Deceleration)               | Decelerating             | Highest deceleration  | Very less deceleration |
| Contact call (Pitch)                      | Lower                    |                       | Higher                 |
| Contact call (Note Duration)              | Longer                   |                       | Shorter                |
| Contact call (Note intervals)             | Longer                   |                       | Shorter                |
| Flight call (Presence of sub-note)        | No                       | No information        | Yes                    |
| Flight call (Pitch)                       | Lower                    | No information        | Higher                 |
| Flight call (Note duration)               | Lower                    | No information        | Higher                 |
| Flight call (Note intervals)              | Lower                    | No information        | Higher                 |
| Drumroll (Speed of delivery) <sup>†</sup> |                          | Faster                | Slower                 |
| Drumroll (Acceleration) <sup>†</sup>      |                          | Accelerating          | Steady                 |

<sup>†</sup> Limited samples

*Chrysocolaptes* are more similar to each other compared to the Himalayan taxa (GC), but strangely ST (and not SO) shows some intermediate characteristics between GC and SO (see Fig. 2, 12). However, ST is not intermediate in morphology. SO differs from GC only slightly in being (a) smaller and more compact, (b) shorter crest, (c) broader black eye-stripe, (d) more bronze back, and (e) larger red rump patch (del Hoyo et al. 2020; Rasmussen & Anderton 2012). ST differs from GC in more striking aspects: (a) darker red upper parts, (b) longer and paler bill, (c) white throat, and (d) more extensive black on face, and neck nearly lacking a white supercilium (Rasmussen & Anderton 2012). Hence, morphologically ST is more divergent from SO and GC, with SO showing some intermediate characteristics. Though not in Aves, there is evidence of reverse colonisation of the Western Ghats by the Sri Lankan fauna (Bossuyt et al. 2018). Could SO be a case of reverse colonisation from Sri Lanka from an ancestral ST? Or has SO developed vocalisation variations due to the presence of other sympatric woodpeckers in the Western Ghats that are absent in Sri Lanka? Only a molecular phylogeny of the Greater Flameback would elucidate the true affinities of these two endemic taxa of South Asia vis-à-vis the more widespread GC.

It is also relevant to call out the plusses and pitfalls of using sound recordings from citizen science databases for studies like the present one. Needless to say, the geographical spread of samples that we obtained from these databases is enormous and the effort/cost for first hand collection by an individual/team is eliminated. However, these recordings have some variability and careful filtering was required before we could use it in our analysis. We do not know if all the recordings have been backed visually and even if they were, whether similar birds like Common Flameback *D. javanese* or Himalayan Flameback *D. shorii* were confidently eliminated. Hence, we did not use recordings whose identity appeared uncertain, and in certain cases, e.g., Drumroll, we reached out to observers to reassign their recordings. Flight calls are tricky as we lacked the information whether the bird was flying in or out relative to the recordist. We did not account for the Doppler effect when the bird is moving as the frequency change would be < 5% (assuming a speed relative to the recordist of 10m/s, after Tobalske 1996). Certain vocalisations, particularly drumrolls, will have a gender bias, and we were not able to ascribe the correct sex to each recording. Hence, the effect of such bias on analysis remains undocumented. Gender assignment of calls would be particularly useful for playback studies.

Voice in woodpeckers is innate, and the voice within the *Chrysocolaptes* genus is poorly differentiated, and thus any significant difference may point towards an important genetic divergence. The obvious and significant vocal difference mentioned by Rasmussen & Anderton (2012) for SO is now confirmed quantitatively and further enhanced by an equally important difference in Flight call. Limited evidence from Drumroll also indicates additional diagnosability. This is all the more astonishing given the limited vocal divergence among species in the genus, and that this suggests a clearly divergent lineage, which may be better treated as a distinct species.

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## References

- Anderson, M. J., 2017 Permutational Multivariate Analysis of Variance (PERMANOVA) Wiley StatsRef: Statistics Reference Online. DOI: <http://10.1002/9781118445112.start.07841>. [Accessed on 25 January 2020.]
- Bossuyt, F., Beenaerts, N., Gower, D. J., Pethiyagoda, R., Roelants, K., Mannaert, A., Wilkinson, M., Bahir, M. M., Manamendra-Arachchi, K., Ng, P. K. L., Schneider, C. J., Oommen, O. V., Milinkovitch, M. C. 2018. Local endemism within the Western Ghats-Sri Lanka Biodiversity Hotspot. *Science* 15: 306 (5695): 479–481. DOI: <https://10.1126/science.1100167>. [Accessed on 25 January 2020.]
- Budka, M., Deonizak, K., Tumiel, T., & Woźna, J. T., 2018. Vocal individuality in drumming in great spotted woodpecker—A biological perspective and implications for conservation. *PLoS ONE* 13 (2): e0191716. DOI: <https://doi.org/10.1371/journal.pone.0191716>. [Accessed on 25 January 2020.]
- Clements, J. F., Schulenberg, T. S., Iliff, M. J., Billerman, S. M., Fredericks, T. A., Sullivan, B. L., & Wood, C. L., 2019. The eBird/Clements Checklist of Birds of the World: v2019. Website URL: <https://www.birds.cornell.edu/clementschecklist/download/>. [Accessed on 25 January 2020.]
- del Hoyo, J., Collar, N., & Christie, D. A., 2020. Greater Flameback (*Chrysocolaptes guttacristatus*), version 1.0. In *Birds of the World* (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. Website URL: <https://doi.org/10.2173/bow.grefla.1.01>. [Accessed on 12 July 2021.]
- Dickinson, E. C., & Remsen, J. V. J., (eds.) 2013. *The Howard and Moore complete checklist of the birds of the world: 1. Non-passerines*. 4th ed. Eastbourne, UK: Aves Press. Vol. 1 of 2 vols. Pp. i–I, 1–461.
- Garcia, M., Theunissen, F., Sèbe, F., Clavel, J., Ravignani, A., Marin-Cudraz, T., Fuchs, J. & Mathevon, N. 2020. Evolution of communication signals and information during species radiation. *Nature Communications* 11: 4970. Website URL: <https://doi.org/10.1038/s41467-020-18772-3>. [Accessed on 25 January 2021.]
- Gill, F., Donsker, D., & Rasmussen, P., (Eds.) 2021. IOC World Bird List (v11.2). DOI: <https://doi.org/10.14344/IOC.ML.11.2>. [Accessed on 25 January 2021.]
- HBW & BirdLife International 2020. Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. Version 5. Website URL: [http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife\\_Checklist\\_v5\\_Dec19.zip](http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v5_Dec19.zip). [xls zipped 1 MB]. [Accessed on 25 January 2021.]
- Martinez, A. P., 2020. pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.4. [Accessed on 1 August 2021.]
- Ramachandran, V., Robin, V. V., Tamma, K., & Ramakrishnan U., 2016. Climatic and geographic barriers drive distributional patterns of bird phenotypes within peninsular India. *Journal of Avian Biology* 48 (5): 620–630. DOI: <https://doi.org/10.5061/dryad.6m668>. [Accessed on 1 August 2021.]
- Rasmussen, P. C., & Anderton, J. C., 2012. *Birds of South Asia: the Ripley guide*. 2nd ed. Washington, D.C. and Barcelona: Smithsonian Institution and Lynx Edicions. 2 vols. Pp. 1–378; 1–683.
- Tobalske, B. W., 1996. Scaling of muscle composition, wing morphology, and intermittent flight behavior in woodpeckers. *Auk* 113: 151–177.