

1 **Structural and functional complexity of vocalizations in a cooperatively breeding passerine, Jungle**

2 **Babbler**

3 Soniya Devi Yambem, Sonam Chorol and Manjari Jain*

4 Department of Biological Sciences, Indian Institute of Science Education and Research, Mohali, India

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7 ***Corresponding Author**

8

9 Address correspondence to:

10 Manjari Jain

11 Department of Biological Sciences,

12 Indian Institute of Science Education and Research, Mohali,

13 Punjab 140306, India

14 manjari@iisermohali.ac.in

15

16 **Abstract:** Animal vocal communication ranges from simple to complex based on repertoire size, structure, and
17 composition of calls and the information encoded in them. According to the social complexity hypothesis,
18 communication complexity tends to increase with an increase in social complexity. While several studies on
19 mammalian systems exist supporting this, evidence from avian systems is comparatively limited. Towards this,
20 we present evidence for complex acoustic communication in a cooperatively breeding passerine, Jungle Babbler,
21 based on three aspects of complexity: an extensive repertoire of acoustically-distinct calls, within-call structural
22 complexity and the diverse behavioural contexts in which these calls are used. Jungle Babblers were found to
23 possess a structurally and functionally diverse vocal repertoire comprising 15 different calls. Detailed acoustic
24 analyses of multisyllabic calls revealed that these calls are composed of different notes. Further, despite a large
25 number of notes present in the repertoire, the number of calls were limited to 15. This implies that there may be
26 underlying rules that determine call composition to give rise to functional calls to which receivers respond. We
27 also found that these calls were produced in a variety of affiliative and agonistic contexts and were employed
28 towards coordination of diverse social behaviours including group movement, foraging, brood care, aggression
29 and vigilance. Yet, 7 out of 15 vocalizations were produced in the context of vigilance. This disproportionate
30 investment of vocalizations towards co-ordinated acoustic vigilance is characteristic of many cooperatively

31 breeding birds. Our study extends support for the social complexity hypothesis and also lays the foundation for
32 future investigations on combinatorial and syntactical rules underlying call structure and function in bird
33 vocalizations.

34

35 **Significance statement**

36 Studies on vocal complexity in birds have focussed mainly on repertoire size, structure and function. However,
37 fine temporal and spectral features of elements that constitute a call/song are rarely examined to evaluate vocal
38 complexity. We examined complex communication in a cooperatively breeding social passerine, Jungle Babbler
39 for which we assessed repertoire size, function, acoustic features of calls and of their constituent elements.
40 Jungle Babblers were found to possess a structurally and functionally diverse vocal repertoire comprising of 15
41 calls, 46% of which were in the context of vigilance, thereby extending support to the social complexity
42 hypothesis. We also found that several calls were composed of multiple, acoustically distinct notes. These
43 findings will be foundational in understanding the interrelations between sociality and communicative
44 complexity and underlying combinatorial rules that determine call structure and function.

45

46 **Keywords:** Vocal repertoire, affiliative call, agonistic call, multisyllabic call, communicative complexity,
47 sociality.

48

49 **Introduction**

50 Theories on the evolution of language have long acknowledged the importance of sociality in the evolution of
51 complex communication. The social complexity hypothesis posits that communication complexity tends to
52 increase with an increase in social complexity (Blumstein and Armitage 1997). This is because social animals
53 are likely to require higher sophistication in communication to coordinate different behaviours and sustain the
54 relationships between individuals within a social group. The complexity of communication is determined by
55 both structural and functional complexity. Structural complexity of vocalizations is determined by the
56 compositional features of calls (how many elements make a call and how these elements are organized within a
57 call), overall acoustic features of the call (temporal and spectral characteristics) and the total number of unique
58 vocalizations of a species (Hailman and Ficken 1986; Zimmermann and Lerch 1993; reviewed in Freeberg et al.
59 2012). Additionally, the different behavioural contexts in which calls differ also add to the communication
60 complexity (reviewed in Freeberg et al. 2012; Crane et al. 2016). Based on the number of elements in a call,

61 avian vocalizations can be classified as monosyllabic or multisyllabic (Rothstein 1988). A ‘syllable’ or ‘note’ is
62 the simplest element of a call and forms the smallest acoustic unit, which when combines with other such units
63 (of the same or different type) forms a ‘phrase’ (multisyllabic call). The total vocalization produced by an
64 animal throughout its lifetime is called a vocal repertoire (Searcy 1992). Repertoire size vary from species to
65 species, for instance, male Common Grackles have only one song type (Searcy 1992) whereas Common
66 Nightingale sings up to 180 different song types (Weiss et al. 2014). A smaller repertoire is considered as less
67 complex compared to a larger repertoire size (Blumstein and Armitage 1997).

68 The function of the call repertoire is different in different species and requires extensive behavioural
69 observations to ascertain. In many species of songbirds, complex vocalizations serve as a sexual display to
70 attract mates or as territorial display against conspecific and heterospecific individuals. It has been shown that
71 individuals with larger repertoire sizes are more successful in attaining mates (Catchpole 1987; Robinson and
72 Creanza 2019) or can hold a territory for a longer duration (Hiebert et al. 1989). It has also been reported that in
73 several species the size of the repertoire increases with complexity in vocalization context. For instance, Diana
74 monkeys produce predator-specific alarm calls (Zuberbühler 2002) whereas, in Meerkats, alarm calls vary
75 depending not only on predator type but also on the level of urgency (Manser 2001).

76 Social animals exhibit higher frequency and diversity of interactions between different individuals than solitary
77 animals and possess a larger and more complex repertoire to deliver meaningful inference (Freeberg et al. 2012;
78 Krams et al. 2012; Leighton 2017). Based on the interaction type, calls are broadly classified as either
79 ‘affiliative’ or ‘agonistic’. Calls that are used in maintaining social bonds are ‘affiliative’ whereas ‘agonistic
80 calls are produced against conspecific and heterospecific rivals (Kondo and Watanabe 2009). Quantifying and
81 categorizing the entire repertoire based on signal structure and function can provide valuable insights into the
82 behaviour of the species and selective forces that drive the evolution of complex communication.

83 Jungle Babblers (*Turdoides striata*) are cooperatively breeding passerines that live in groups of 3-20 individuals
84 and are widely distributed throughout lowland India, both in rural and urban habitats (Andrews and Naik 1970;
85 Gaston 1977; Ali and Ripley 1978). Group members engage in many social behaviours such as cooperative
86 brood care, sentinel duty, collective foraging, anti-predator behaviour, allogrooming and intergroup
87 confrontations. (Andrews and Naik 1970; Gaston 1977). To maintain bonding within the social group, it is
88 expected that there would be vocalizations associated with interactive behaviours, thereby raising the possibility
89 that Jungle Babblers possess a complex communication system. Andrew and Naik (1970) and later Gaston
90 (1977) provided onomatopoeic descriptions of some vocalizations of the species and the situation in which the

91 calls were observed, thereby raising the possibility of complex acoustic communication in this cooperative
92 breeder. However, so far, no study has examined complex acoustic communication in Jungle Babblers, despite
93 their broad distribution, the potential for multiple vocalizations and known social system. In this study, we aim
94 to examine complex acoustic communication in Jungle Babblers by a quantitative and systematic investigation
95 of the vocal repertoire of the species. The major objectives were 1. To quantify the acoustic structure of calls to
96 estimate the number of structurally distinct call types, 2. To determine the acoustic features of the constituent
97 elements (notes / syllables) of each of these call types 3. To ascertain the behavioural context associated with
98 each call type through extensive behavioural observations. This study provides the first acoustic characterization
99 of the vocalization of Jungle Babblers, carried out both across and within call type, and the associated
100 behavioural contexts. Apart from providing the bedrock for future investigations of vocal complexity in this
101 species, this study will allow a comparative investigation of complex communication in avian systems with
102 varying degrees of sociality and ecological conditions.

103

104 **Materials and methods**

105 Since the data collected for this study was completely based on observations and recordings of animals in the
106 field, it was not possible to record data blind.

107 **Study site**

108 The study was conducted in Mohali region, located in the eastern part of Punjab in northern India (30°36' and
109 30°45'N latitude and 76°38' and 76°46'E longitude), which covers an area of about 116.50 km². According to
110 the Koppen-Geiger climate classification system, the climate of Mohali comes under the 'Cwa' category (Kottek
111 et al. 2006). Mohali has a humid subtropical climate that is variable throughout the year with a hot summer and
112 cold, dry winter separated by a brief period of tropical monsoon climate. The habitat of the study site comprised
113 of shaded gardens and closed-canopy woodland with trees such as *Populous deltoides*, *Ficus religiosa*, *F.*
114 *glomerata*, *Vachellia nilotica*, *Morus alba*, *M. nigra*, and *Psidium guajava*, *Leucaena leucocephala*, *Chukrasia*
115 *tabularis*, *Callistemon sp.*, and shrubby habitats dominated by bushes of *Lantana camara*, *Ricinus*
116 *communis* and *Cannabis sp.* (Fig. S1).

117 **Behavioural data collection**

118 The fieldwork for this study was conducted between May 2016 and March 2020, during which we carried out
119 systematic behavioural observations to interpret the context of vocalizations of Jungle Babblers. All behavioural
120 observations were made on free-ranging birds using 8 x 42 binoculars (Nikon, Monarch 7) following *Ad*

121 *libitum* and focal animal sampling (Altman 1974). Towards this, the vocalizing individual was identified and its
122 behaviour was noted. This was accompanied by noting the behaviour of all group members in sight and a quick
123 scan of the environment. Any response given to the signaller was also noted.

124 **Acoustic data collection**

125 Recordings were taken from free-ranging Jungle Babblers in their natural habitat at a distance of up to 10 meters
126 from the caller. A solid-state recorder (Marantz PMD661MKII; frequency response: 20 Hz – 20 kHz), connected
127 to a super-cardioid shotgun microphone (Sennheiser ME66 with K6 PM; frequency response: 40 Hz to 20 kHz),
128 covered with a foam windscreen (Sennheiser MZW66) was used to record all vocalizations (sampling rate of
129 44.1KHz and 16-bit accuracy). Calls of nestling were recorded while they were inside the nest and from
130 fledgling outside the nest. Fledglings were identified based on iris colour (juvenile – black; adult – pale white;
131 Fig. S2). Recordings were also made from individuals trapped in mist-net and during their subsequent release.
132 To minimize the overlap of calls between individuals, recordings were focused on a single individual except for
133 chorus calls. While recording the vocalizations, the behaviour of the caller and receivers were noted as
134 described above and the surroundings were scanned. These observations were announced at the end of the call
135 recording. Data from the behavioural observations were then used to interpret the context of vocalizations and
136 the recordings were categorized under these behavioural categories. Andrew and Naik (1970) and Gaston (1977)
137 catalogued a list of situations in which Jungle Babblers vocalize. This list served as a valuable reference library
138 for validating our independent inferences.

139 **Acoustic analyses**

140 A total of 303 recordings comprising of 1895 calls were processed in Raven Pro 1.5 (Cornell Laboratory of
141 Ornithology, USA) and spectrograms were generated using Hann window function, size 512 with a 50%
142 overlap. After generating the spectrograms, only those calls with no or minimum overlap were retained for
143 further analysis except in the case of chorus calls. For the acoustic categorization of calls, as a first step, calls
144 were classified under the same or different call type based on aural and visual inspection of the spectrograms.
145 Calls were also examined based on the inter-note interval. If the time gap between two notes was ≤ 0.1 s, they
146 were considered to belong to the same call (Catchpole and Slater 2010). This allowed us to categorize all call
147 types under one of two categories: ‘monosyllabic’ (single note call) or ‘multisyllabic’. The third category of
148 calls called ‘chorus calls’ included those vocalizations in which multiple individuals vocalized simultaneously.
149 Within each of these three categories detailed acoustic characterization of different calls was then carried out
150 based on 7 different acoustic features: A) spectral parameters i) frequency 5% (Hz) ii) frequency 95% (Hz) iii)

151 bandwidth 90% (Hz) and iv) peak frequency (Hz); B) temporal parameters: i) call duration (s) and ii) inter-
152 note/syllable interval (s) iii) total number of notes in a call. Finally, all multisyllabic calls were subjected to
153 further analyses wherein a total number of notes in each call was identified and acoustic analyses of each
154 constituent note were carried out based on all spectral parameters and note duration. For the analyses of the
155 chorus calls, only spectral parameters were considered as signal overlap from different callers made analyses of
156 temporal features unreliable.

157 **Statistical analysis**

158 Calls that were preliminarily categorized under different call types based on behavioural observation and audio
159 and visual observation of the spectrogram. They were then subjected to rigorous statistical analyses based on
160 their acoustic features, as determined by the signal analyses carried out. For this, pairwise comparisons were
161 carried out between calls belonging to the same category (monosyllabic, multisyllabic or chorus calls). Calls
162 were considered to be different from each other if they differed significantly in at least 1 out of the 7 acoustic
163 parameters examined. Further, within call complexity was examined for all multisyllabic calls by examining
164 whether a given call was composed of multiple, acoustically distinct notes or was composed of repeats of the
165 same elements. All the statistical analysis was carried out in Statistica 64 (Dell Inc.2015, Version 12). To check
166 for normality of data, the Shapiro-Wilk's test was used. ANOVA, and Kruskal-Wallis ANOVA were performed
167 for data that followed and did not follow a normal distribution, respectively. Further, for pairwise comparisons,
168 unpaired t-test for normally distributed data and Mann-Whitney U (MW U) test for data that did not follow
169 normal distribution were carried out. This allowed us to examine if the behavioural categorization of calls as
170 different call types was consistent with the acoustic characterization and to examine the complexity of vocal
171 repertoire both across and within call types.

172

173 **Results**

174 **Vocal repertoire and structural complexity of calls**

175 The audio-visual inspection of the spectrogram and analyses of inter-note interval resulted in Jungle Babbler
176 vocalizations being classified into 15 different call types. Adult vocalizations included 5 monosyllabic, 6
177 multisyllabic and 2 chorus calls, whereas juvenile vocalizations included 2 call types, both of which were
178 monosyllabic (Fig. 1, Table 1). All monosyllabic adult calls were found to be significantly different from each
179 other based on their acoustic features (Kruskal-Wallis ANOVA; Table S1a). The pairwise comparison revealed
180 that all calls were significantly different from each other by at least three acoustic parameters (MW U test; Table

181 S1b, Fig. 2a-e). The two Juvenile calls were significantly different from each other only in temporal
182 characteristics and not based on any spectral parameters (t-test and MW U test; Table S2, Fig. 2f).

183 Similarly, there was a significant difference between all multisyllabic calls based on their acoustic features
184 (Analysis of variance; Table S3a and Kruskal-Wallis ANOVA; Table S3b; Fig. 3). The pairwise comparison
185 showed that all multisyllabic calls are also significantly different from each other (t-test and MW U test; Table
186 S3c and d Fig.3) by more than one parameter.

187 The two chorus calls were found to be not significantly different based on their spectral features (t-test and MW
188 U test, Table S4a and b).

189 Based on aural and visual inspection, we found that each multisyllabic call was composed of different note
190 types, which were then compared statistically within a call type. Multisyllabic calls were found to be composed
191 of at least three acoustically distinct note type each (Analysis of Variance, Kruskal-Wallis ANOVA and MW U
192 test; Table S5a-c; Fig. 4 and 5).

193 **Behavioural context of vocalizations**

194 This large and structurally complex vocal repertoire of Jungle Babblers was also found to be functionally
195 diverse. The results from the behavioural observations suggest that these vocalizations are produced in 2 major
196 functional contexts: affiliative and agonistic. Detailed below are the behavioural contexts in which the signallers
197 were observed to produce these diverse vocalizations.

198 **Affiliative calls**

199 i) Contact (Chack) call: This call is used to contact conspecifics and is produced when an individual is
200 separated from the group. In response to this call, a member of the group gives the same call back and
201 eventually approached the left behind signaller leading to a reunion of a diverted individual with the rest of the
202 group. This is a loud call that consists of only one note (monosyllabic) with faintly visible harmonics (Fig. 1a).

203 ii) Foraging (Cuk) call: This is a very soft call produced by one or more individuals of the group while
204 foraging on the ground/leaf litter. No unique behaviour or reaction was observed when this call is produced and
205 the group continues to forage. This monosyllabic call is the call with the shortest duration (Fig. 1b).

206 iii) Prompt (Ca-ca-ca) call: This call is given by an adult heading towards nest for food provisioning.
207 Nestlings respond to this call with a 'begging call' (described later). The call is multisyllabic, mainly composed
208 of 3 - 4 notes that are similar spectrally, however, note duration decreases progressively (Fig. 1c).

209 iv) Prompt flight (Long cu-cu-cu) call: This vocalization is also made when adults are in proximity to
210 fledglings, typically around nests. While producing these calls, adults take short flights from one position to

211 another and back to the fledgling. This seems to prompt fledgling movement. Fledglings were observed to move
212 out of the nest or move from their current location to another in response to this call by adults. This
213 multisyllabic call is usually produced by more than one individual at a time and is composed of the most number
214 of notes (3 – 11 notes per call). The notes at the beginning of the call are of longer duration and higher peak
215 frequency and forthcoming notes show a gradual decrease in both these parameters (Fig. 1d).

216 v) Flight (Cu-cu-cu) call: This call is generally produced during group displacement. The call is initiated
217 by one individual and is eventually joined in by the rest of the group members. Group movement initiates soon
218 after. This is a soft multisyllabic call composed of 3 – 4 notes. Here too, notes in the beginning, have a longer
219 duration and higher frequency 95% while trailing notes progressively become shorter in duration and have lower
220 values for frequency 95% (Fig. 1e).

221 vi) Fledgling close (Chack) call: This vocalization is produced by fledglings or juveniles in close
222 proximity to adults. Adults do not respond to this call. Spectrally, this monosyllabic call is almost similar to
223 adult contact call however, adult contact calls are shorter in duration than these calls (Fig. 1f).

224 vii) Begging call: Nestlings and fledglings produce this monosyllabic call during food provisioning and in
225 response to prompt calls. Spectrally, this call is very dynamic. This call is generally accompanied with the wide
226 opening of beak and rigorous flapping of wings (Fig. 1g).

227 **Agonistic calls**

228 viii) Sentinel soft (Low chack) call: This monosyllabic call is exclusively produced by a sentinel- an
229 individual on vigilance duty, on an elevated perch, forgoing foraging while the rest of the group members
230 forage, Andrews and Naik (1970). While producing this vocalization, the caller is generally not very alert and
231 may even groom at times. There is no visible change in the behaviour of group members in response to this call
232 (Fig. 1h).

233 ix) Threat (Shriek) call: This call is produced in response to the sudden approach of a potential threat. Both
234 the caller and receiver usually respond instantly with a startle and take shelter in the closest tree or foliage. After
235 a while, inside the cover, they might start grooming or allogrooming or resume regular behaviour (generally
236 foraging). This call is monosyllabic but sometimes two notes may be produced in continuation. Among all
237 monosyllabic calls, this call has the highest peak frequency (Fig. 1i).

238 x) Distress (Kya-kya-kya) call: This is a loud monosyllabic call produced repeatedly by an individual in
239 distress. Such a situation may arise when an individual gets trapped in mist-net or is handled by a human or a

240 predator. This call attracts group members towards the caller. Among all monosyllabic call, this call has the
241 highest note duration (Fig. 1j).

242 xi) Alert (Cackle) call: During intrusion by any potential threat, a perched individual produces this call,
243 accompanied by periodic hops from one side to the other, flapping of wings and twitching of tail up and down.
244 This call may induce other members of the group to join in the vocalization, whereas on other occasions no
245 visible response from the group members is observed. This call is a multisyllabic call comprising of 2 – 4
246 different notes. As the call proceeds, there is a decrease in note duration and minimum frequency (frequency
247 5%) whereas the frequency bandwidth (bandwidth 90%) increases progressively (Fig. 1k).

248 xii) Harsh (Khack) call: This is a noisy harsh call, produced by any perched individual in response to any
249 intrusion which is not an immediate threat, including the observer. This call is also produced while individuals
250 are foraging in the foliage or are in the queue for food provisioning. There was also no visible response by group
251 members in response to this call. This call is multisyllabic and comprises of 1-5 notes forming a phrase (Fig. 1l).

252 xiii) Intermediate alert (Khack cackle) call: Any perched individual produces this call in the presence of the
253 observer but also for other intruders. The intensity of the caller's behaviour is somewhat intermediate to the
254 harsh and alert call. No visible response was observed from the group. The call comprises of 6 structurally
255 different notes/syllables with highest call duration (Figure 3j and 3k). Moreover, there is no fixed pattern in the
256 composition of the call (Fig. 1m).

257 xiv) Mobbing (Wheezy cackle) call: This vocalization is a chorus call wherein more than one individual at a
258 time is involved. It was observed to be produced in the presence of an immediate and proximate predator such
259 as domestic/feral cats, Indian Grey Mongoose, Greater Coucal, Spotted Owlet, Barn Owl, snakes, and Bonnet
260 Macaque. While making this call, all individuals involved, flutter around and 'harass' the potential predator
261 until the predator retreats. However, if the predator did not move from its position, then the group disperses
262 from the location. This vocalization also attracts neighboring heterospecific birds to join in mobbing the
263 predator accompanied by loud and urgent vocalizations. It may, however, be noted that while producing
264 mobbing calls, Jungle Babblers were not observed making any physical interactions with the predator (Fig. 1n).

265 xv) Intergroup fight (guttural noise) call: This is also a chorus call, produced when two different groups of
266 Jungle Babblers come in contact with each other. They produce this vocalization while moving from one tree to
267 another, chasing each other. Along with this vocalization, sometimes individuals engage in mid-air physical
268 fights, striking each other using beaks and claws while falling to the ground, after which they usually disengage.
269 Concurrently other members of the groups surround the fighting pair while producing this vocalization. They

270 also make this call by positioning themselves facing each other on different trees without physical interaction. It
271 may be noted, however, that intergroup fights are rare (Fig. 1o).

272

273 **Discussion**

274 The major drivers of vocal complexity in avian systems include sexual selection and sociality (MacDougall-
275 Shackleton 1997; Freeberg et al. 2012) and measures of complexity include both structural (repertoire size and
276 features of calls) and functional (behavioural contexts) aspects of vocalizations (Crane et al. 2016; Holt 2017).

277 Cooperative breeding has been found to be a strong predictor of large repertoire size in avian systems (Leighton
278 2017) and several avian cooperative breeders possess multiple structurally-distinct calls (Ficken et al. 1978;
279 Seddon 2002; Warrington et al. 2014; Crane et al. 2016). Evaluation of overall structural complexity, however,
280 must also incorporate an assessment of the fine structure of all vocalizations by measuring the temporal and
281 spectral features of elements (notes/syllables) that constitute a call/song. This level of analysis is largely missing
282 in the assessment of vocal complexity in social birds (Greig et al. 2008; Grieves et al. 2015; Crane et al. 2016).

283 In this study, we examined communicative complexity in Jungle Babblers by examining repertoire size, overall
284 acoustic features of all calls, and their constituent elements, and the behavioural contexts in which vocalizations
285 are produced. The vocal repertoire of Jungle Babblers comprises of 7 monosyllabic and 8 multisyllabic calls. All
286 calls were structurally distinct from each other. Note-level analyses within multisyllabic calls revealed that each
287 call were constructed by the combination of several acoustically distinct notes (call type (number of distinct
288 notes): prompt (3), flight (3), prompt flight (4), alert (4), harsh (4), intermediate alert (6)). While 31 notes were
289 recorded in the vocal repertoire of this species, the functional repertoire size is limited to 15 calls. This implies
290 that this large variety of notes combine in a limited number of ways to form meaningful calls. It is also possible
291 that some of the notes are shared across different calls and examining this would require across call note
292 comparisons. This study thereby lays the foundations to further investigations on understanding the limits of
293 combinatorial rules that determine the composition of meaningful multisyllabic calls in this social bird.

294 With respect to the functional aspects of the vocal repertoire, our findings are consistent with the observations of
295 Andrews and Naik (1970) and Gaston (1977) that various affiliative and agonistic behaviours are mediated by
296 vocalizations in Jungle Babblers. Affiliative calls include those that coordinate group movement as well as food
297 provisioning and brood care. For instance, flight call in Jungle Babblers clearly induces all group members to
298 cohesively displace to a new location and contact call functions to reunite lost or left-behind members with the
299 rest of the group. Calls like prompt and prompt flight induce fledglings to beg and fly, respectively. Similar

300 findings have been reported in Pied Babblers that produces ‘purrs’ that prompt fledglings towards a food source
301 and ‘clucks’ to induce group displacement (Engesser et al. 2017). The exact function of the foraging call in
302 Jungle Babblers remains unclear. We speculate that similar to foraging calls in Pied Babblers, this call may play
303 a role in maintaining the spacing between the foragers in order to enhance foraging efficiency (Radford and
304 Ridley 2008).

305 Our findings also suggest that 8 out of 15 vocalizations of Jungle Babblers are produced in agonistic context
306 towards conspecifics and heterospecifics. It includes inter-group fight calls (guttural noise) produced against
307 conspecific rivals and 6 others, including threat, distress, harsh, intermediate alert, alert, and mobbing calls that
308 are produced against heterospecifics, mainly potential predators. This disproportionately high representation of
309 calls towards vigilance could be because predation imposes a strong selective pressure by directly impacting the
310 fitness of an individual (Leighton 2017). It is known that vigilance behaviour is costly since the animals must
311 interrupt foraging in order to scan the environment for predators (Wickler 1985). By having coordinated
312 acoustic vigilance, individuals can mitigate this cost as it renders visual scans by every individual unnecessary.
313 This, however, is contingent on the animals producing reliable alarm calls, allowing receivers to choose the
314 appropriate escape strategy, thereby increasing the chance of survival (Marler 1967). Thus, it would be useful to
315 have functionally referential alarm vocalizations that inform the receivers about the category of predator (aerial
316 or terrestrial or even predator specific; Seyfarth et al. 1980; Naguib et al. 1999). It would also be useful to
317 encode the level of urgency (encoding distance of potential threat) to allow the receivers to respond in an
318 appropriate time (Manser 2001). All of these together is likely to increase the proportional representation of
319 vigilance vocalization in the vocal repertoire of cooperative breeders. Meerkats, for instance, are known to
320 possess 30 different vocalizations of which 18 (60%) are produced in the context of vigilance. Similar to our
321 findings, studies on other cooperatively breeding birds have shown that a large number of vocalizations are
322 dedicated to vigilance. This includes Chestnut-crowned Babblers (4 out of 13 calls; Crane et al. 2016), Pale-
323 winged Trumpeter (5 out of 12 calls; Seddon et al. 2002) and Black-capped Chickadees (5 out of 11 calls;
324 Ficken et al.1978). In a study carried out on 253 bird species across the globe, representing 59 families, it was
325 found that cooperative breeders dedicated a significantly higher proportion of their vocal repertoire to vigilance
326 related vocalizations (Leighton 2017).

327 Alarm calls can be categorised into three main types: flee, mob and distress (reviewed in Magrath et al. 2015).
328 Flee-type calls are generally short duration pure tone calls making them difficult to localize (Marler 1955). In
329 Arabian Babblers, alarm calls produced by foragers were found to be much shorter as compared to those

330 produced by sentinel, since foragers were only able to witness the threat in proximity whereas sentinel perceived
331 it from a distance (Sommer 2011). Our results also suggest that the alarm vocalizations produced by foragers,
332 threat call, is monosyllabic with the shortest note duration and functions as a flee call. However, alarm calls like
333 harsh, intermediate alert and alert produced by sentinel or individuals on perch were found to be multisyllabic
334 calls. We speculate that different alarm calls of Jungle Babbler - harsh, intermediate alert and alert are produced
335 in relation to low, intermediate and high urgency of the threat, however, this needs further examination. We
336 speculate that the sentinel soft call could serve the function similar to the 'watchman song' reported in other
337 cooperative breeders (Wickler 1985, Manser 1999, Hollén et al. 2008). The 'watchman song' is a form of
338 acoustic coordination between vigilant (sentinel) and non-vigilant (foragers) group members, which serves as a
339 proxy for the presence of sentinel on duty for the rest of the group (Wickler 1985). It can be considered as both
340 affiliative and agonistic as it helps in maintaining group cohesion as well as provides information about the
341 predation risk (Kern and Radford 2013).

342 Overall, our study on the social behaviour and acoustic communication of a sexually monomorphic,
343 cooperatively breeding passerine, Jungle Babbler, extends support to the social complexity hypothesis. The
344 broad distribution of this species in India and its disproportionate investment in vigilance calls make it a good
345 model system to study vigilance behaviour in groups occupying diverse habitats with disparate predation
346 pressures. The quantitative categorization of different call types to note level in our study has rarely been carried
347 out. This along with the information on variation in the acoustic features of notes provides a rich database for
348 future research on understanding rules governing multisyllabic call composition and information encoding in
349 avian vocalizations. While the overall behavioural contexts of the vocalizations are evident from our findings,
350 understanding the proximate function of some of the vocalizations such as the foraging, sentinel soft and
351 intermediate alert will require further studies, including manipulative experiments using field playbacks. This
352 study will be foundational to all such future investigations.

353

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363 **Author contributions**

364 MJ conceived and designed the study. SDY carried out all the field work and acoustic analyses for repertoire
365 size, call characteristics and for behavioural data. SC carried out all the field work and acoustic analyses for note
366 level complexity. SDY, SC and MJ carried out all statistical analyses and wrote the manuscript. All authors
367 approved the final version of the manuscript.

368 **Data availability**

369 The datasets generated are available as supplementary material

370 **Compliance with ethical standards**

371 **Conflict of interest**

372 The authors declare that they have no conflict of interest.

373 **Ethical approval**

374 Jungle Babblers are listed in Schedule IV under the Indian Wildlife Protection Act (1972) and designated as
375 'Least Concern' by IUCN's Red List of Threatened Species. This study was conducted with necessary permits
376 (No. 3625) from Department of Forest and Wildlife Preservation, Government of Punjab, India, and with the
377 approval of Institute Animal Ethical Committee (IISER/SAFE/PRT/2018/003), IISER Mohali, India. No
378 animals were harmed or kept in captivity for this study.

379

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- 457

458 **Table 1** Temporal and spectral characteristics of 15 vocalizations type of Jungle Babbler showing mean \pm std. N and n correspond to the number of recordings and calls for
 459 each call types respectively. Blue colour filled cells represent affiliative call category and unfilled represent agonistic call category. * represent onomatopoeic description
 460 used by Gaston (1977)

S. no	Call types		N	n	No. of notes	Call duration (s)	Inter-note interval (s)	Frequency 5% (kHz)	Frequency 95% (kHz)	Frequency bandwidth 90% (kHz)	Peak frequency (kHz)
	Behavioural context	Onomatopoeic description									
1	Contact	Chack *	33	175	1	0.13 \pm 0.02	-	1.75 \pm 0.28	3.76 \pm 0.41	2.02 \pm 0.55	2.68 \pm 0.22
2	Fledgling close	Fledgling chack	10	41	1	0.15 \pm 0.02	-	1.58 \pm 0.26	4.28 \pm 0.98	2.70 \pm 1.01	2.66 \pm 0.34
3	Begging	Begging	14	78	1	0.24 \pm 0.05	-	1.42 \pm 0.4	4.82 \pm 0.83	3.40 \pm 0.98	3.01 \pm 1.05
4	Foraging	Cuk *	17	63	1	0.05 \pm 0.01	-	0.92 \pm 0.13	5.73 \pm 0.71	4.81 \pm 0.67	1.67 \pm 0.60
5	Prompt	Ca-ca-ca	19	47	4.45 \pm 1.4	0.31 \pm 0.13	0.04 \pm 0.01	0.91 \pm 0.19	5.75 \pm 1.40	4.84 \pm 1.36	1.59 \pm 0.35
6	Flight	Cu-cu-cu *	31	79	3.68 \pm 0.65	0.30 \pm 0.06	0.05 \pm 0.01	0.89 \pm 0.28	4.26 \pm 0.67	3.36 \pm 0.80	1.81 \pm 0.45
7	Prompt flight	Long cu-cu-cu	22	60	7.07 \pm 3.88	0.55 \pm 0.31	0.04 \pm 0.01	0.92 \pm 0.20	4.60 \pm 0.97	3.68 \pm 1.06	1.67 \pm 0.35
8	Threat	Shriek *	12	17	1	0.1 \pm 0.02	-	2.33 \pm 0.38	6.00 \pm 0.88	3.67 \pm 0.82	4.11 \pm 1.33
9	Sentinel soft	Low chack	21	99	1	0.1 \pm 0.02	-	1.02 \pm 0.16	4.95 \pm 0.95	3.92 \pm 0.99	2.35 \pm 0.46
10	Distress	Kya-kya-kya	22	220	1	0.32 \pm 0.06	-	1.88 \pm 0.20	5.25 \pm 1.1	3.37 \pm 1.14	3.04 \pm 0.71
11	Alert	Cackle *	23	363	4.14 \pm 2.91	0.54 \pm 0.34	0.05 \pm 0.01	1.58 \pm 0.33	6.46 \pm 0.72	4.87 \pm 0.76	3.45 \pm 0.95
12	Harsh	Khack	38	332	1.57 \pm 0.78	0.34 \pm 0.25	0.07 \pm 0.02	1.36 \pm 0.30	5.50 \pm 1.17	4.14 \pm 1.02	2.73 \pm 0.85
13	Intermediate alert	Khack cackle	19	299	2.98 \pm 1.26	0.90 \pm 0.30	0.06 \pm 0.01	1.67 \pm 0.21	5.81 \pm 0.79	4.14 \pm 0.67	3.27 \pm 0.80
14	Mobbing	Wheezy cackle *	15	15	-	-	-	1.85 \pm 0.12	6.40 \pm 0.55	4.55 \pm 0.53	4.12 \pm 0.58
15	Inter-group fight	Guttural noise *	7	7	-	-	-	1.63 \pm 0.31	6.05 \pm 0.38	4.42 \pm 0.40	3.89 \pm 0.48

461 **Figure Legends**

462

463 **Fig.1** Spectrograms of different call types of Jungle Babbler. **Affiliative calls:** **a** contact; **b** foraging; **c** prompt;
464 **d** prompt flight; **e** flight; **f** fledgling close and **g** begging. **Agonistic calls:** **h** sentinel soft; **i** threat; **j** distress; **k**
465 alert; **l** harsh; **m** intermediate alert; **n** mobbing and **o** intergroup fight

466

467 **Fig. 2** Variation in different monosyllabic call types of adult and juvenile of Jungle Babblers based on 5
468 different acoustic parameters. **Adult calls:** **a** call duration; **b** frequency 5%; **c** frequency 95%; **d** bandwidth 90%
469 and **e** peak frequency. **Juvenile calls:** **f** call duration. Roman numbers on the x-axis correspond to different call
470 types: **i** contact; **ii** sentinel soft; **iii** threat; **iv** distress; **v** foraging; **vi** begging; and **vii** fledgling close. Different
471 alphabets represent the statistical difference between call types. Bar corresponds to mean with 95% confidence
472 interval

473

474 **Fig. 3** Variation in different multisyllabic calls of adult based on 7 acoustic parameters. **a** number of notes; **b**
475 inter-note interval; **c** call duration; **d** frequency 5%; **e** frequency 95%; **f** bandwidth 90%; and **g** peak frequency.
476 Roman numbers on the x-axis correspond to different call types; **i** alert; **ii** harsh; **iii** intermediate alert; **iv** flight;
477 **v** prompt flight; and **vi** prompt. Different alphabets represent the statistical difference between call types. Bar
478 corresponds to mean with 95% confidence interval

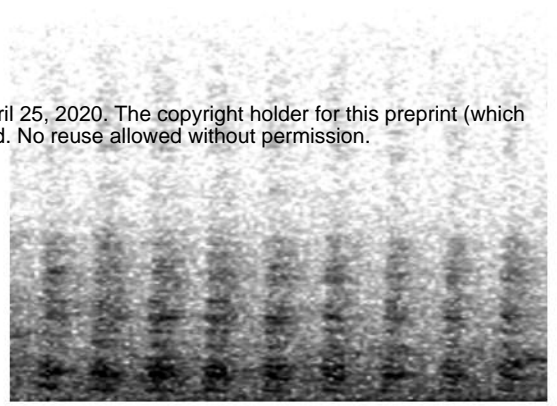
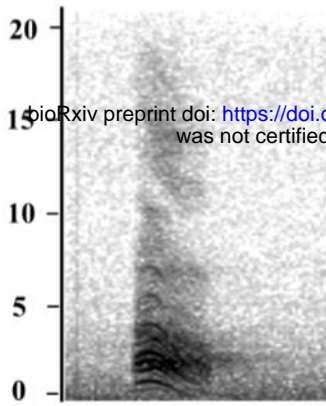
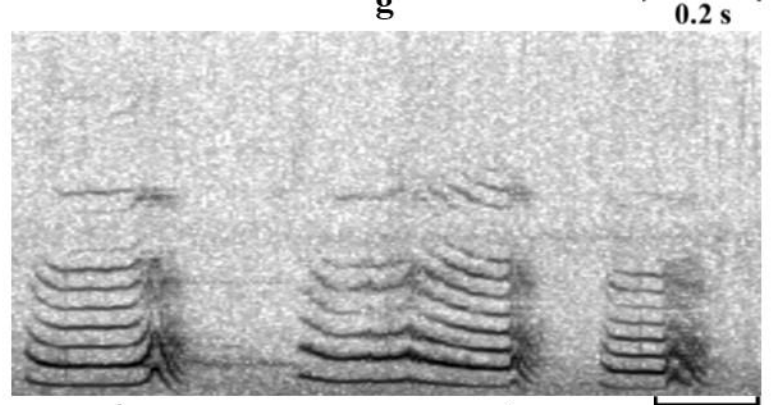
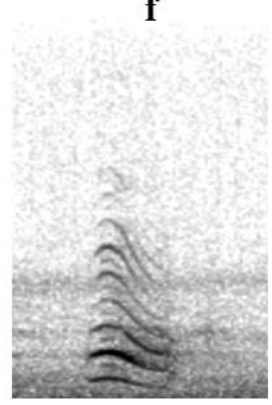
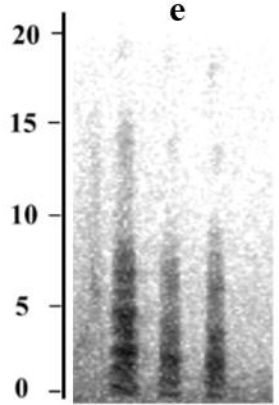
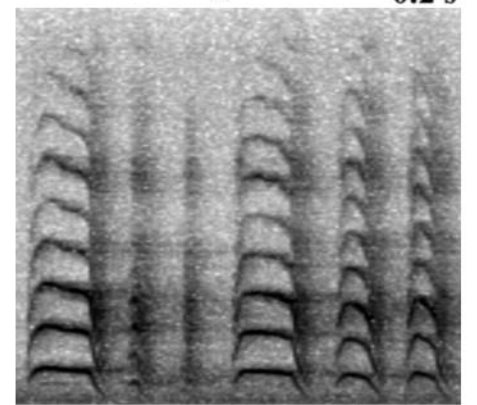
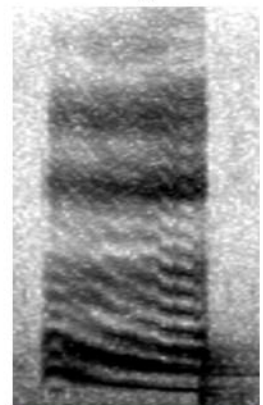
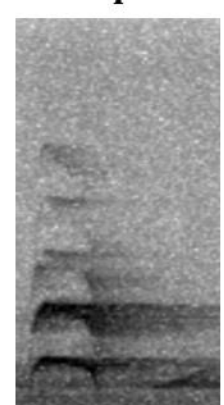
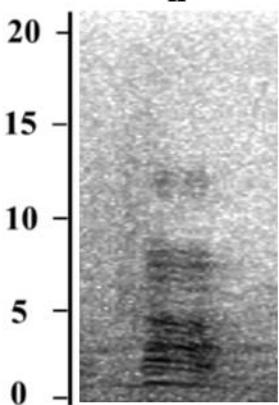
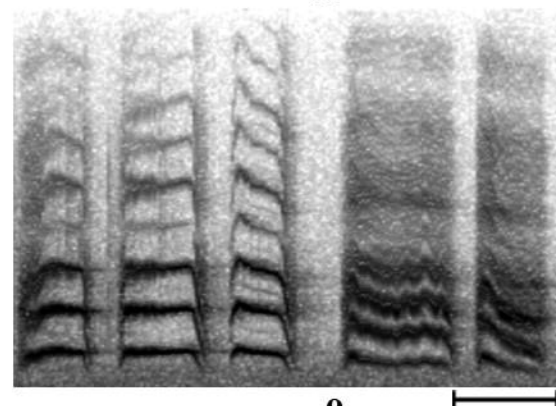
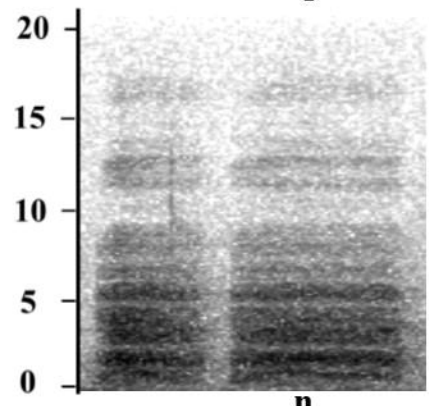
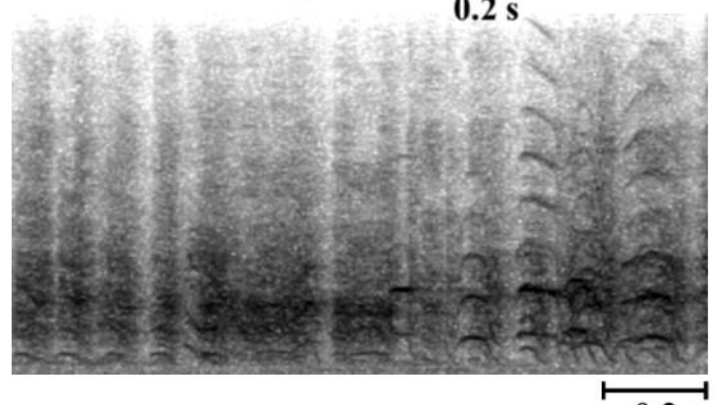
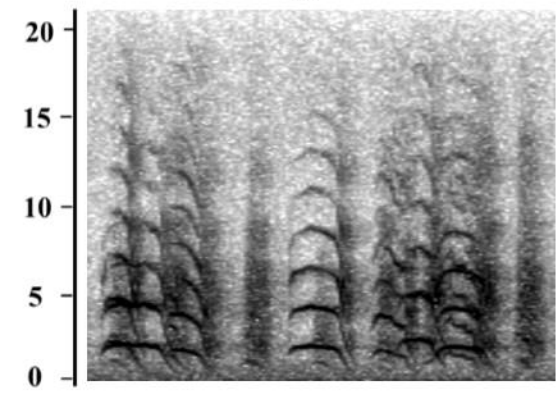
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480 **Fig. 4** Variation in notes within multisyllabic affiliative call. **a** note duration of 4 note types of prompt call; **b**
481 note duration and **c** frequency 95% and bandwidth 90% of 3 note types of flight call; and **d** note duration and **e**
482 peak frequency of 7 note types of prompt flight calls. Different alphabets represent the statistical difference
483 between call types. Bar corresponds to mean with 95% confidence interval

484

485 **Fig. 5** Variation in notes by temporal and spectral parameter within multisyllabic agonistic calls. **a** note duration
486 and **b** frequency 5% and bandwidth 90% of 4 note types of alert call; **c** note duration and **d** frequency 95%,
487 bandwidth 90% and peak frequency of 6 notes of harsh call; and **e** note duration, **f** frequency 5% and frequency
488 95% and **g** bandwidth 90% and peak frequency of 6 note types of intermediate alert call. Different alphabets
489 represent the statistical difference between call types. Bar corresponds to mean with 95% confidence interval

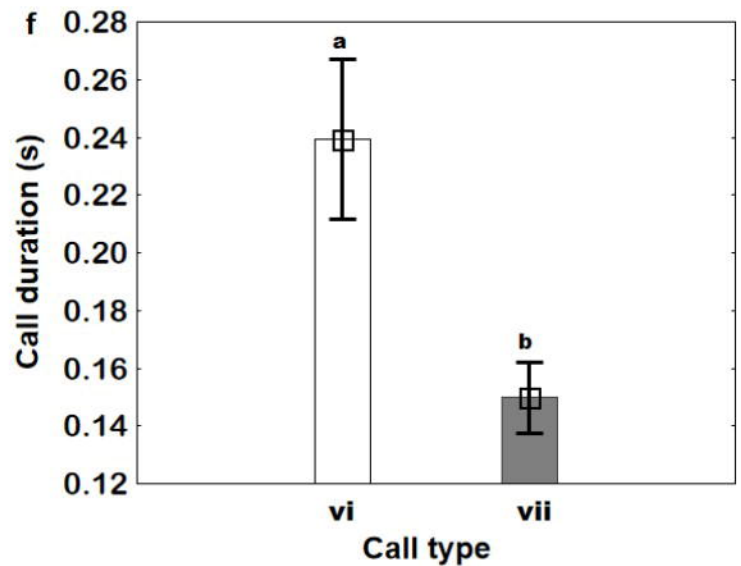
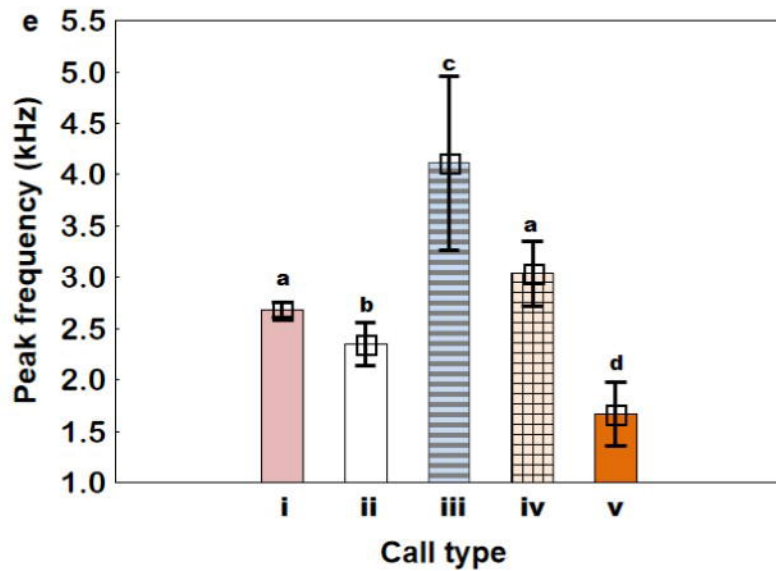
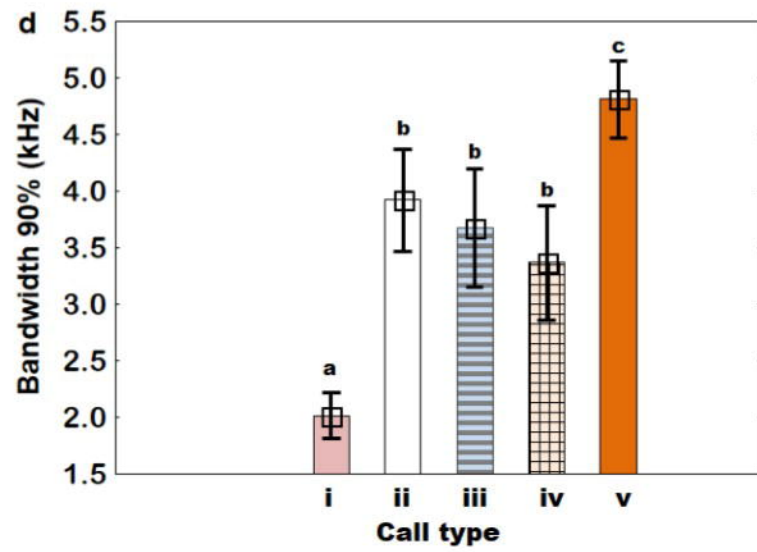
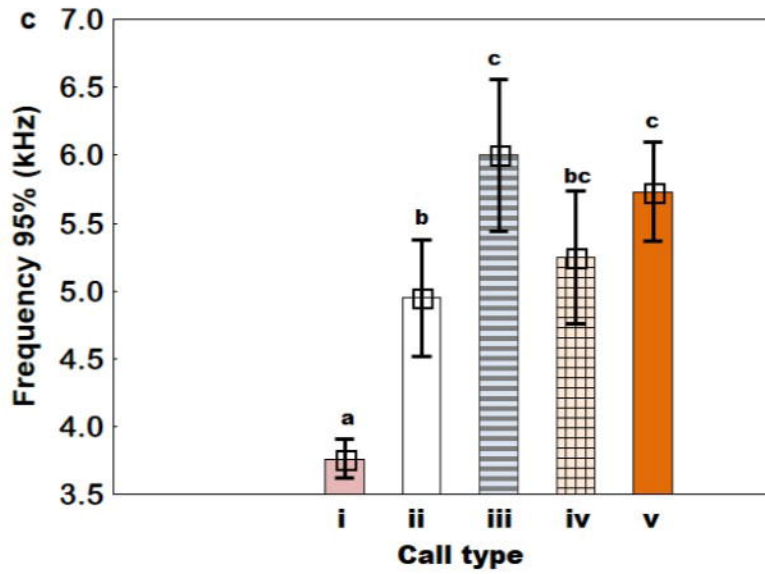
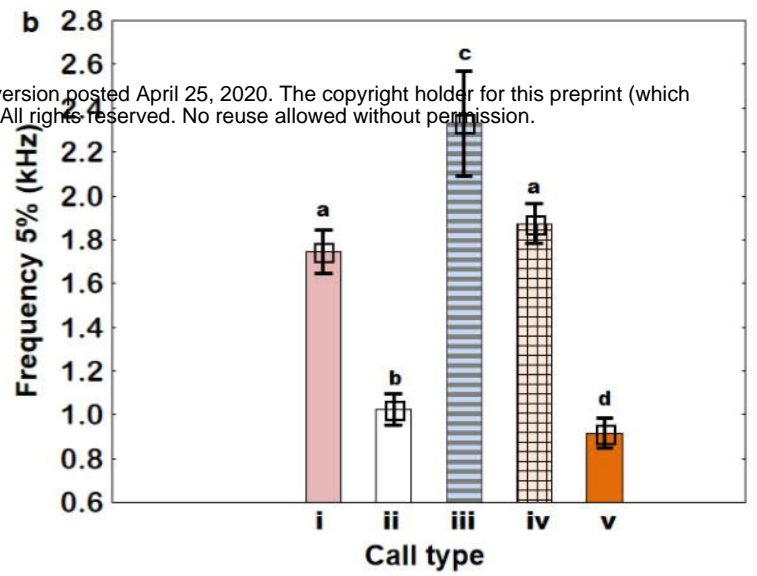
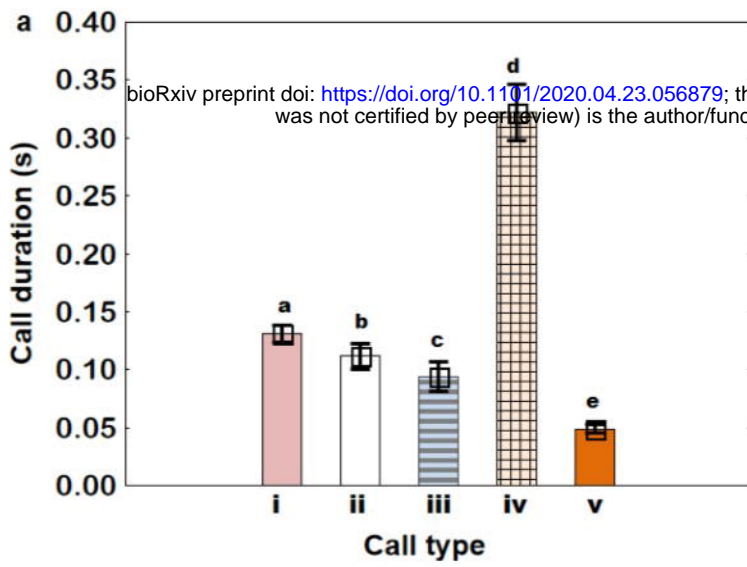
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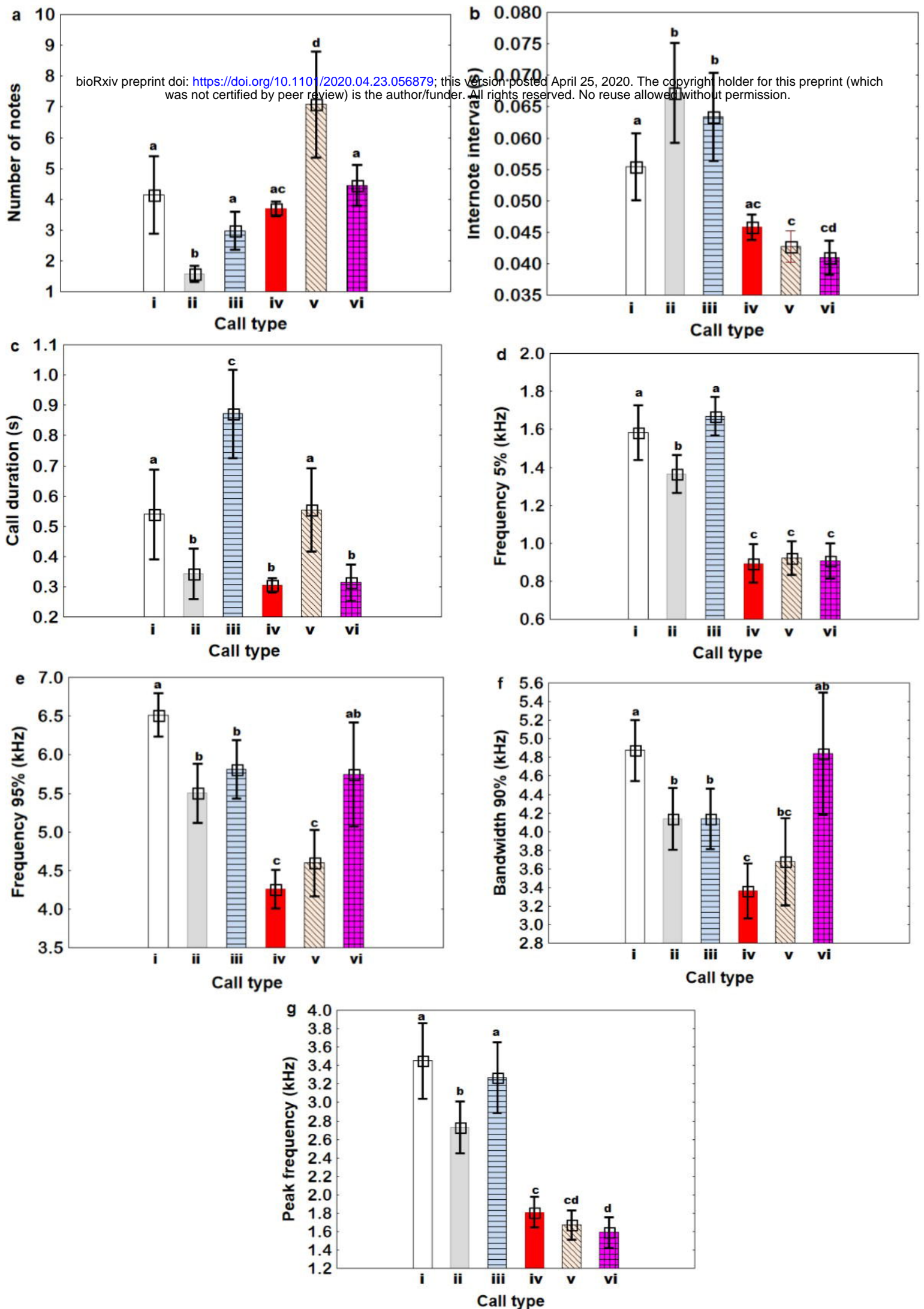
a**b****c****d****e****f****g****h****i****j****k****l****m****n****o**

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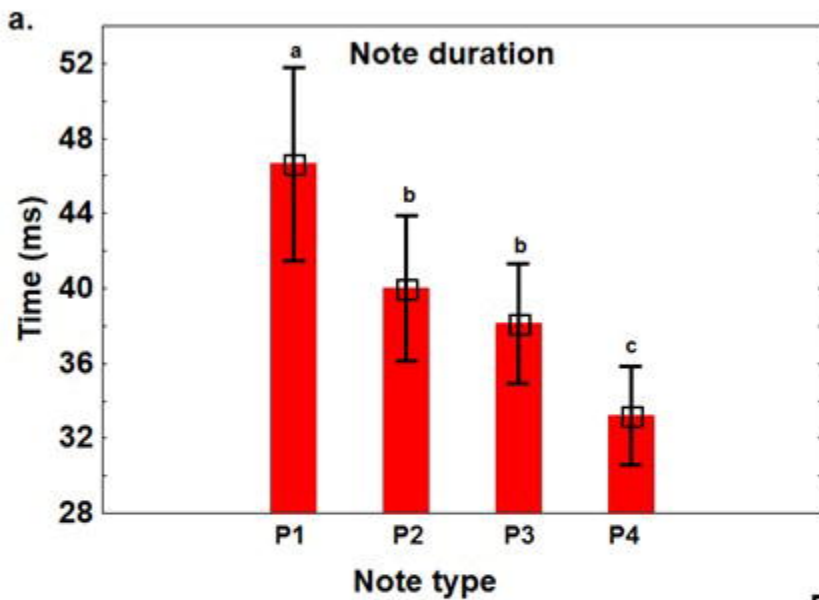
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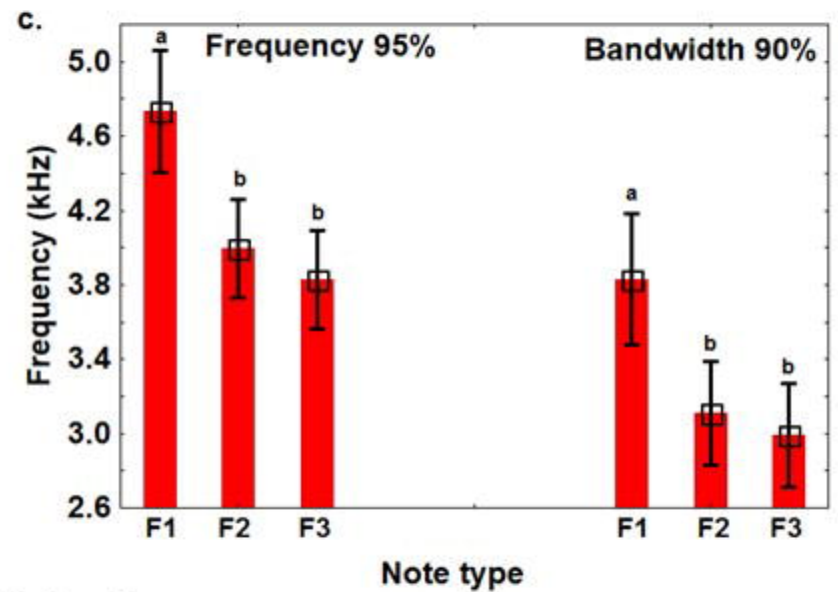
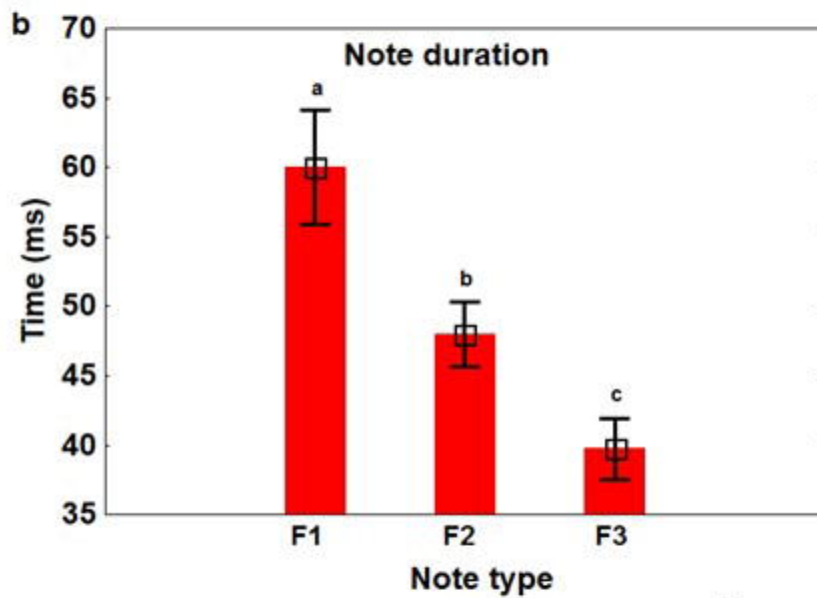




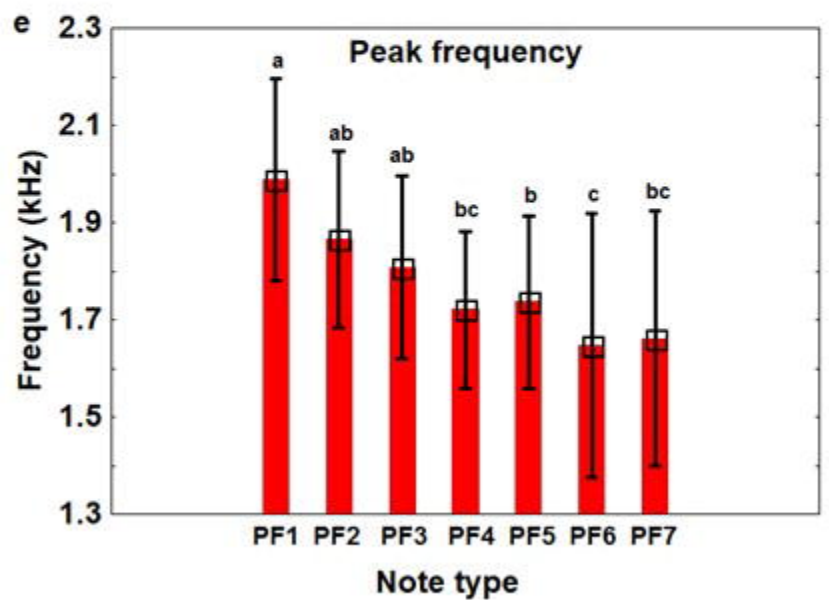
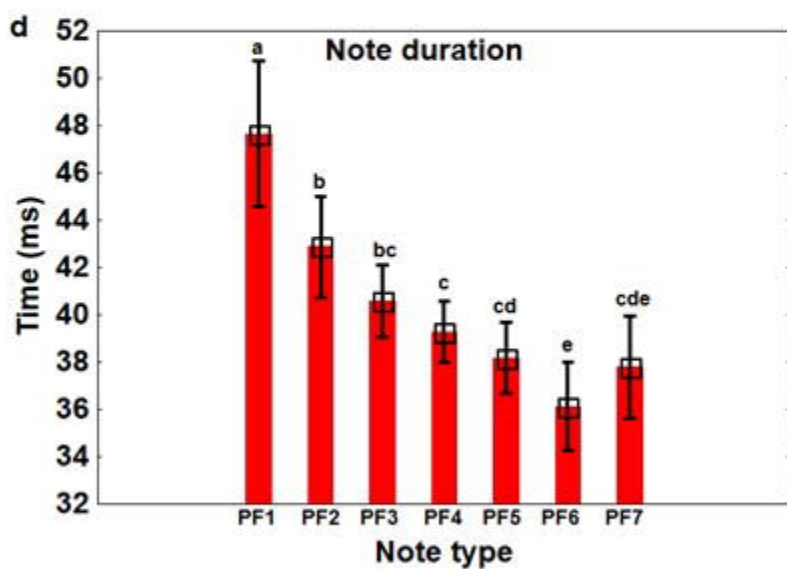
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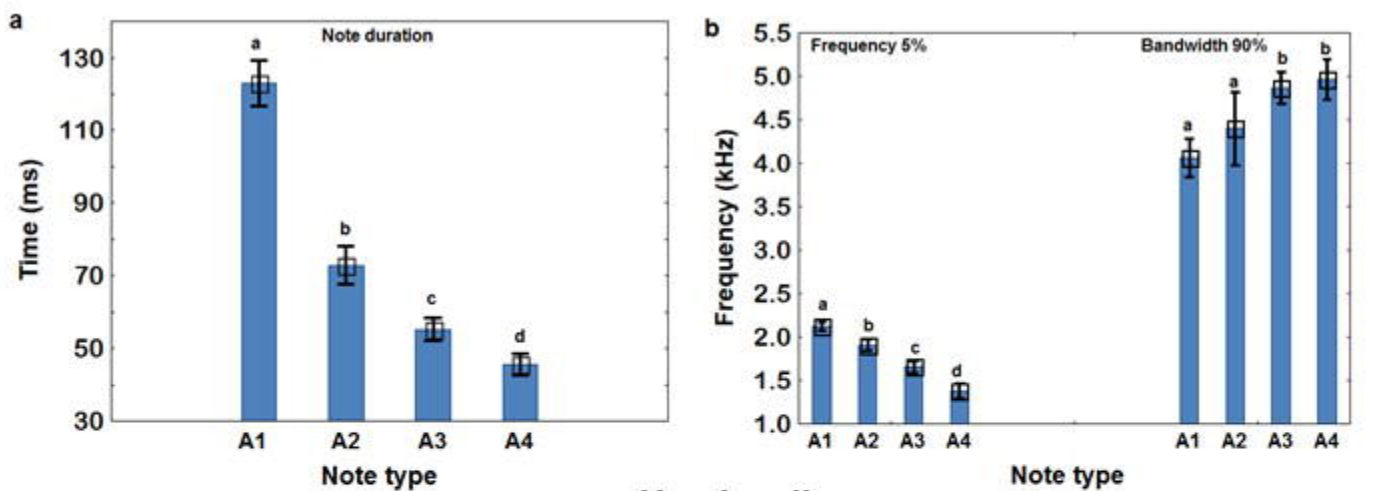
Flight call



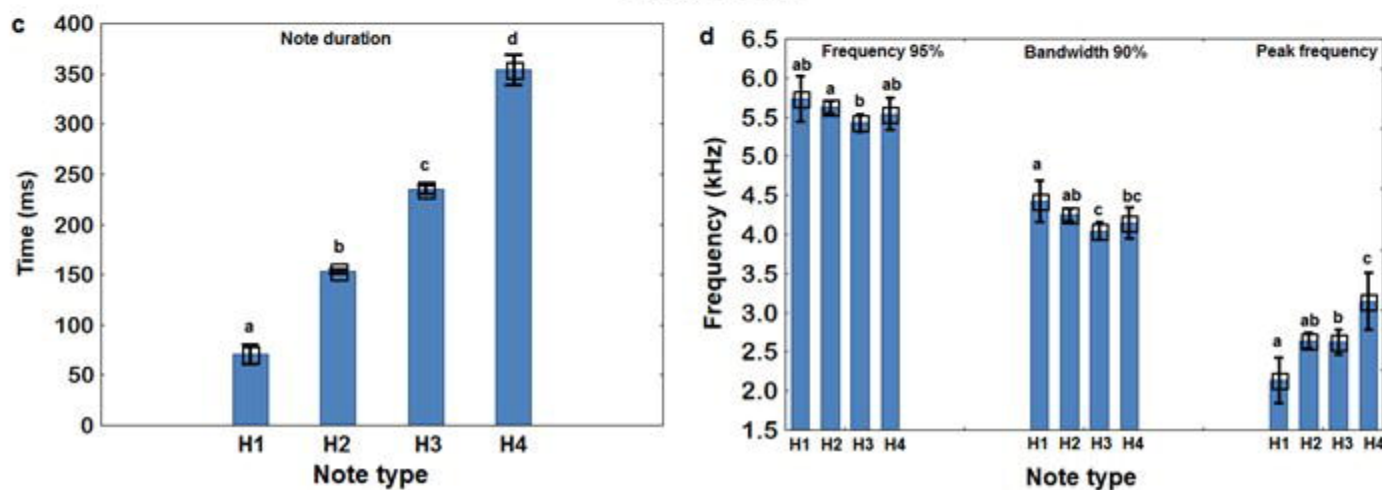
Prompt flight call



Alert call



Harsh call



Intermediate alert

