Vocal cues to identity

Vocal cues to identity: pied babblers produce individually distinct but not stable loud calls

David J. Humphries[1,4] (corresponding author), Fiona M. Finch[4], Matthew B. V. Bell[2,4], Amanda R. Ridley[1,3,4,5]

[1] Department of Biological Sciences, Macquarie University, NSW, Australia

[2]Instittute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3JT, UK

[3]DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, University of Cape Town, Western Cape, South Africa

[4]Pied Babbler Research Project, Kuruman River Reserve, South Africa

[5]Centre for Evolutionary Biology, School of Animal Biology, University of Western Australia, WA, Australia

Correspondence: david.humphries@mq.edu.au

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Abstract

Reliable cues to identity are an important component for the successful coordination of social behaviours in group living animals. Coordinating social behaviours over long distances becomes problematic, as cues to identity are often limited to one or two sensory modalities. This limitation can often select for strong individuality in those cues used for long distance communication. Pied babblers, *Turdoides bicolor*, produce a number of different types of 'loud calls' which are frequently used to signal to individuals beyond the range of visual or olfactory pathways of communication. Here we show that three of these 'loud call' types: the v-shaped chatter, the double note ascending chatter, and the atonal chatter, are each individually distinct. We hypothesise that individuality in the three loud call types tested here may represent a possible pathway to social recognition in this species that may have important consequences for social interactions. However, we also found that the atonal chatter was unstable between years suggesting that this particular call type may not be a reliable long-term indicator to identity.

Introduction

The ability to recognise and classify individuals either as kin, mate, neighbour or rival is likely to be advantageous (Sherman et al. 1997). Correct recognition of these classes may reduce the cost of agonistic competition, increase the opportunity for kin directed altruism, and decrease the risk of costly inbreeding (Barnard & Burk 1979; Tibbetts & Dale 2007). It has been suggested that many animals that engage in complex social behaviours often display distinctive phenotypic characteristics to facilitate recognition (Tibbetts 2004; Pollard & Blumstein 2011). In birds,

vocalisations are often the dominant form of communication (Halpin 1991) and 'vocal signatures' to both identity (Price 1998; Seddon et al. 2002; Sharp & Hatchwell 2005; McDonald et al. 2007; Kennedy et al. 2009) and kinship have been found (Sharp & Hatchwell 2006; McDonald & Wright 2011). Reliable cues to identity may be particularly important in animals that engage in cooperative tasks with others, as it can allow individuals to maximise their direct or indirect fitness by recognising and avoiding cheats or by preferentially assisting kin (Bradbury & Vehrencamp 2011).

Among highly social birds, individuality has been found in a variety of vocalisation types including contact calls (Sharp & Hatchwell 2005), lost calls (Seddon et al. 2002), mobbing calls (Kennedy et al. 2009), provisioning calls (McDonald et al. 2007), and song (Price 1998). Individuality in these calls may play an important role in coordinating social behaviours. For example, long tailed tits, are able to recognise familiar kin from their vocalisations, and use these cues to preferentially assist at the nests of close relatives (Sharp et al. 2005). Recognition speed and accuracy may be improved by combining information from multiple sensory modalities (Amedi et al. 2005). With 'loud call' vocalisations (also referred to as 'long distance calls'), the receiving individual may often be out of range to perceive visual or olfactory cues of identity, the receiver is reliant on the identity signals within the vocalisation in order to evaluate caller identity (Schleidt 1973; Mitani et al. 1996; Darden et al. 2003; Slabbekoorn 2004). Vocal individuality, where inter-individual call variation is greater than intra-individual variation (Falls 1982), may be under particularly strong selection in loud calls due to: (a) its function in the coordination of social behaviours, and (b) the limits on the number of communication pathways available over long distances.

Under some circumstances there may be extended periods between the previous and current encounter between the signalling individual and the receiver. Here it is not just important that the signalling individual produces a cue to identity, but also that those cues remain stable through time. For instance, the black-legged kittiwake produces individually distinct loud calls that are used for mate recognition and may be used to relocate a breeding partner at the beginning of each breeding season (Wooller 1978; Aubin et al. 2007). The use of vocalisations to relocate breeding partners after months of separation may necessitate the selection for identity cues that are reliable from year to year. However, in a number of studies where vocalisations have been found to be individually distinct over short periods, those vocal characteristics that defined an individual changed through time (Jorgensen & French 1998; Ellis 2008). It is therefore important to ascertain how stable cues to identity are through time.

The Southern pied babbler, *Turdoides bicolor*, is a highly social and territorial species from southern Africa that produces a range of different loud call vocalisations (Golabek 2010). Here we investigate whether the loud calls of the Southern pied babbler are both (a) individually distinct when collected within one week of each other, and (b) distinctive from one year to the next. Previous work has identified that pied babblers produce eight acoustically distinct loud call types that are used in a variety of both inter- and intra-group social situations (Golabek 2010). These loud calls are characteristically one or two syllables that are repeated for up to 80 seconds in duration (see methods). Loud calls can be given by any member of the social group, but all eight call types are most commonly produced by a dominant group member (Golabek 2010). Here we have focused our analysis on three of these loud call types, the ‘v-shaped chatter’, the ‘double note ascending chatter’, and the

98 'atonal chatter' (see figure 1). These three call types were chosen as they were the
99 most frequently observed and recorded of the eight call types. We also investigate
100 the stability of one of the loud calls, the atonal chatter, to test how reliable it may be
101 as a cue to identity through time. The atonal chatter was chosen because it was the
102 most frequently observed of the call types across the two observation years. Given
103 that loud calls are often meant for long distance communication, and that pied
104 babblers are a highly social species, we hypothesise that these three call types will
105 have lower intra-individual call variation than inter-individual call variation, which may
106 facilitate the correct recognition of individuals. We also expect these calls to be
107 reliable indicators of identity through time by having lower call variation from one
108 year to the next than variation between individuals.

109

110 **Methods**

111 **Study population and Sound Recording**

112 We recorded the loud calls from a population of pied babblers located at the
113 Kuruman River Reserve in the southern Kalahari desert, South Africa (26º57'S
114 21º49'E) (see Ridley & Raihani 2007 for more details about the study site). Each
115 member of the study population is individually identifiable using a unique
116 combination of colour bands. These medium-sized (70-95g) cooperatively breeding
117 passerines are habituated to close observation, allowing sound recordings to be
118 collected within 5-10 metres of the calling bird. Vocalisations were recorded between
119 October 2010 and April 2012 using a Marantz PMD660 data recorder (2008 D&M
120 Holdings Inc.) and a Seinheisser ME66 shotgun microphone with a K6 power module
121 (2004 Sennheiser), housed in a Rycote pistol grip with windshield to reduce

122 background wind noise. Recordings were collected at a sampling rate of 44.1 kHz, to
123 16-bit WAVE files (.wav). We recorded a minimum of six loud call vocalisations of the
124 same call type from an adult bird within a seven day period. This was to try to
125 minimise any acoustic changes that may have been brought on by changes in
126 physical condition, age or environmental conditions. To test whether calls were
127 reliable indicators to identity through time, we re-recorded individuals a minimum of
128 one year on, again collecting a minimum of 6 calls within seven days. None of the
129 individuals that were re-recorded experienced a change in dominance status, a
130 factor that has been found to affect vocal characteristics in other species (Rukstalis
131 et al. 2003). All calls were collected during the wet season (September-April) to
132 minimise acoustic changes resulting from seasonal variation in physical condition.
133 We also compared the weights of the birds at the time of recording across the two
134 field seasons as a measure of change in physical condition. Focal birds were
135 habituated to the use of a weighing scale by rewarding this behaviour with small
136 amounts of egg and mealworm. Weights were collected for each focal bird using an
137 Ohaus CS200 flat-topped weighing scale (Ohaus, UK) at the start of each recording
138 session (accuracy ±0.1g).
139
140 ***The three call types***
141 The three loud call types analysed, the v-shaped chatter, the double note ascending
142 chatter and the atonal chatter, were all given in a variety of social contexts. However,
143 we have limited our analysis to calls of the same call type given in the same social
144 context.
145

146 The v-shaped chatter is given predominantly as a solo call by the dominant male in
147 both inter and intra-group social contexts. We observed that strings of v-shaped
148 chatter calls lasted for 7.37±0.46 seconds on average (mean±SD; range 1.8-59.0).
149 Our acoustic analysis of the v-shaped chatter was conducted on a total of 81 'v-
150 shaped chatter' calls collected from 8 individuals (average number of calls per focal
151 bird 10.13±5.17 SD).
152
153 The double note ascending chatter is mostly frequently observed as a solo call by
154 the dominant male in both inter and intra-group social contexts (Golabek 2010). We
155 observed calling bouts of the double note ascending chatter lasting 8.02+0.44
156 seconds on average (mean±SD; range 1.1 – 40.1). For the 'double note ascending
157 chatter', we were able to collect 87 calls from 8 different individuals for our analysis.
158 We measured a minimum of six calls from each focal bird, with an average of
159 10.87±6.73 (mean±SD) calls per focal bird.
160
161 The 'atonal chatter' can be given by either sex, and is the most common female solo
162 loud call in the pied babbler (Golabek 2010). It is typically given in intra-group social
163 interactions (Golabek 2010). Calling bouts of the atonal chatter were 6.12±0.33
164 seconds long on average (mean±SD; range 2-25). Our analysis was conducted on
165 147 atonal chatter calls collected from 15 individuals. We collected an average of
166 9.73±3.43 (mean±SD) calls per focal bird in the first year of recording. We recorded
167 the atonal chatter calls from seven individuals at least one year on. 64 calls were
168 collected from these seven individuals in year one (average number of calls per
169 individual 9.14±3.28 SD) and 57 calls in season two (with an average of 8.14±4.18
170 calls per individual; mean ± SD).

171

172 **Sound Analysis**

173 Acoustic analysis was carried out in the bio-acoustic software package 'Raven Pro
174 v1.4' (Cornell lab of Ornithology, www.birds.cornell.edu/raven). For the 'v-shaped
175 chatter' and the 'atonal chatter' we took the 20th call in the call sequence, and for the
176 'double note ascending chatter' we cut the 15th pair of syllables, taking the long and
177 short syllables separately for analysis. If these calls were marred by background
178 noise we cut the next clear call in the sequence. The calls in the call sequence are
179 typically erratic for the first few seconds, we have chosen the 20th and 15th syllables
180 as these appeared to represent points of consistent stability in the respective call
181 sequences. Spectrogram windows were drawn in a Hamming window (512 point,
182 with an overlap of 96.9%). A band pass filter between 500Hz and 22050 kHz was
183 used to eliminate any low frequency noise in the recordings. Each syllable was
184 manually selected and four parameters were automatically measured. The four
185 measurements were; first quartile frequency, aggregate entropy, the centre
186 frequency, and peak frequency (see Charif et al. 2009 for more information on these
187 call parameters). These call parameters were chosen because they showed a lack of
188 outliers and were not collinear with the other terms included (VIFs < 7; Allison 1999).
189 Call duration was measured by hand, resulting in a total of five measurements for
190 each call.

191

192 **Statistics**

193 Call parameter measurements were used to test for individuality using discriminant-
194 function analysis (DFA) performed in the statistical package SPSS statistics, version

19.0 (SPSS Inc., IBM 2012). Our sample sizes here were limited to a minimum of six calls per individual. The DFA has a tendency to overestimate classification when the number of parameters exceeds the minimum number of cases (Tabachnick & Fidell 2001). We therefore limited the number of call parameters in each analysis to five parameters. The percentage of correctly classified cases after leave-one-out cross-validation from the DFA was tested for significance using a binomial test performed in SPSS.

To test for the consistency of vocal identity signatures, a DFA was run on the atonal chatter calls collected in the first year of study. The discriminant functions developed from those calls were then used to assign a predicted calling individual to the calls collected in the second year. We then established the percentage that had been assigned to the correct individual and followed this up with a binomial test performed in SPSS (testing observed classification rate versus what we would expect by chance). The average weights for each focal bird from the first year of recording were compared against the weights of the second year using a paired t-test to test for changes in the mass of the recorded birds between years.

Results

(a) The 'v-shaped chatter'

The DFA was able to correctly classify the v-shaped chatter in 50.0% of cases after leave-one-out cross-validation (DFA, Wilks Lamda = .100, X^2_{35}= 167.250, P=<0.001) indicating significant individuality in the parameter measurements recorded.

(b) The 'double note ascending chatter'

For the double note ascending chatter, both syllables proved to be individually distinct. The short syllable could be correctly classified in 53.2% of cases after leave-one-out cross validation (DFA, Wilks Lamda = 0.121, X^2_{30} = 151.103, P=<0.001), and The long syllable could be correctly classified in 61.5% of cases after leave-one-out cross-validation (DFA, Wilks Lamda = .159, X^2_{30}= 130.512, P=<0.001),

(c) The 'atonal chatter'

Atonal chatter calls were individually distinct and could be correctly classified in 42.7% of cases using leave-one-out cross validation (DFA, Wilks Lamda = 0.057, X^2_{70}= 377.947, P=<0.001).

(d) Consistency of individual call signatures

Using a subset of the atonal chatter calls from year one, they were again found to be individually distinct and could be correctly classified in 43.8% of cases after leave-one-out cross-validation (DFA, Wilkes Lamda =.167, X^2=101.959, df=30, P=<0.001). Additionally, the calls collected one year on in the second season were also individually distinct and could be correctly classified in 56.1% of cases after leave-one-out cross-validation (DFA, Wilkes Lamda =.093, X^2=118.696, df=30, P=<0.001). However, calls collected in the second year were only classified in 12.3% of cases by the discriminant functions produced from the calls of the first year (binomial test, P=0.288). This demonstrates that there is as much variation within the calls collected from an individual between two different years as exists between individuals and

suggests that the atonal chatter may be an unreliable cue to identity through time. The change in vocalisations occurred despite no significant change in the weights of the calling birds between the two recording sessions (paired t-test, P=0.86).

Discussion

Vocal individuality, where variation within the calls of an individual is lower than variation among individuals (Falls 1982), was found in all three of the loud call types tested here (the v-shaped chatter, the double note ascending chatter and the atonal chatter). Distinctive cues to identity are the foundation of recognition and are required for the identification of individuals, kin, neighbours, parent-offspring, rivals, and species (Sherman et al. 1997). Our findings that at least three of the call types of the pied babbler are individually distinct suggest a potential pathway to social recognition in this species that may be used to facilitate social interactions. Social recognition allows individuals to be selective in whom they cooperative with, which can both reduce cheating in mutualistic interactions, as well as increasing indirect fitness benefits when preferentially assisting kin (Bradbury & Vehrencamp 2011).

Recognition has been described as a three-step process; (1) a signalling individual must produce reliable cues to identity, (2) a receiver must detect these cues, and then (3) cognitively make a connection between the cue and the identity (Sherman et al. 1997). The production of vocal cues to identity can facilitate recognition at many levels, allowing both individual recognition as well as the recognition of familiar relatives (Halpin 1991). For example, in emperor penguins individuality in parental calls allows parents and offspring to relocate one another in a crowded colony (Robisson et al. 1993), and in the cooperatively breeding long-tailed tit, individually

distinct calls are used to recognise familiar kin and direct helping behaviours towards closely related individuals, which is likely to have inclusive fitness benefits (Hatchwell et al. 2001; Sharp & Hatchwell 2005; Sharp et al. 2005). Pied babblers coordinate many of their social behaviours, such as the spacing between foraging individuals, and the coordination of sentinel bouts through vocalisations (Radford & Ridley 2007; Hollén et al. 2008; Bell et al. 2010). Our findings that pied babblers produce vocal cues to identity demonstrates a potential pathway to recognition of both individuals and familiar kin in this species which may help further facilitate the coordination of social interactions, although whether they can discriminate between these calls remains to be tested.

Vocalisations are often highly plastic and acoustic structures may change in response to age, physical (Gouzoules & Gouzoules 1990; Bertucci et al. 2012), social (Farabaugh et al. 1994; Mathevon et al. 2010), motivational (Morton 1977), and environmental factors (Patricelli & Blickley 2006; Slabbekoorn & den Boer-Visser 2006). Our findings that the atonal chatter was not a stable long-term indicator to identity demonstrated that this call is also plastic, changing over the course of a year. The changes in the atonal chatter may represent a form of honest signalling where vocalisations change in response to changes in the physical and social status of the calling bird. We found no significant changes in the body mass of the focal birds between the two seasons, but vocal changes may correlate with other physical factors such as age (Green 1981; Blumstein & Munos 2005; Ey et al. 2007) or fatigue (Vannoni & McElligott 2009). Voice breaking has been noted in several species of birds and it is possible that the vocal shifts observed in the atonal chatter may correspond to the ageing of the birds (Radford 2004; Klenova et al. 2010). Here

292 we controlled for social factors by only using calls from individuals that were
293 subordinates in both recording seasons, but it is possible that the changes in the
294 identity signals reflected changes in social status within the subordinate ranks.
295 Instability in the atonal chatter may have important consequences for its reliability as
296 an identity cue over the long term. This could impact on the social behaviour and
297 may require either frequent contact between individuals, or alternative cues to
298 identity to be used in order for long-term recognition to occur. The atonal chatter call
299 is most often observed in intra-group social interactions (Golabek 2010). The use of
300 the atonal chatter call within the social group and the frequent contact that occurs
301 between group members may keep group members updated on changes occurring
302 within individual signatures. However, atonal chatter calls have also been observed
303 from prospecting individuals (D. Humphries, *personal observation*). In the pied
304 babbler, long-term recognition is likely to be important for inbreeding avoidance
305 because they are a long–lived species and may need to find mating partners many
306 years after initial dispersal from the natal territory (Nelson-Flower et al. 2012).
307 Unstable identity labels could potentially lead to costly recognition errors such as
308 inbreeding, if kin recognition in this species is based on prior association. However,
309 research has indicated that inbreeding is rare in this species (Nelson-Flower et al.
310 2012), and therefore it is possible that other cues (such as different call types or
311 signals) may act to allow inbreeding avoidance in this species.
312
313 To conclude, we have found that pied babblers produce three individually distinctive
314 call types that have the potential to act as cues for social recognition. We also found
315 that the atonal chatter was not a reliable indicator to identity from one breeding

season to the next, although the causality of these vocal changes currently remains unclear.

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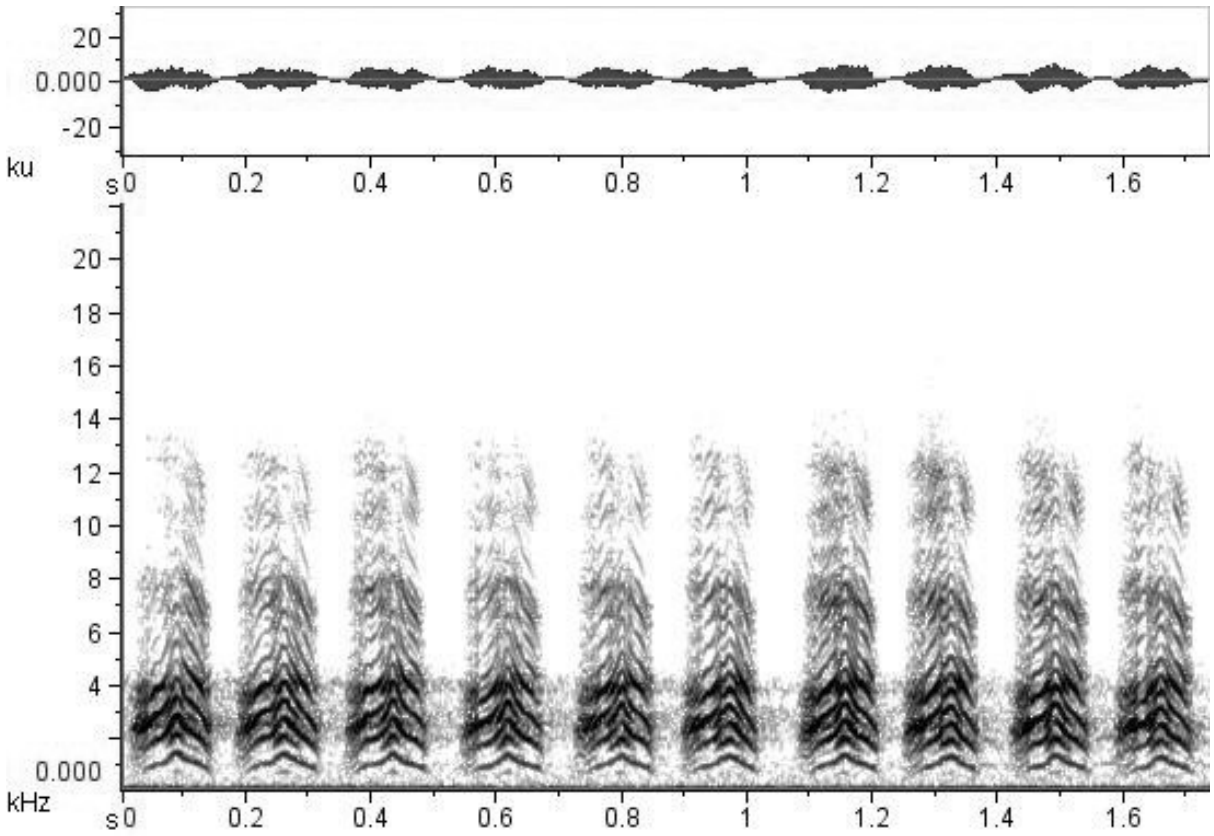
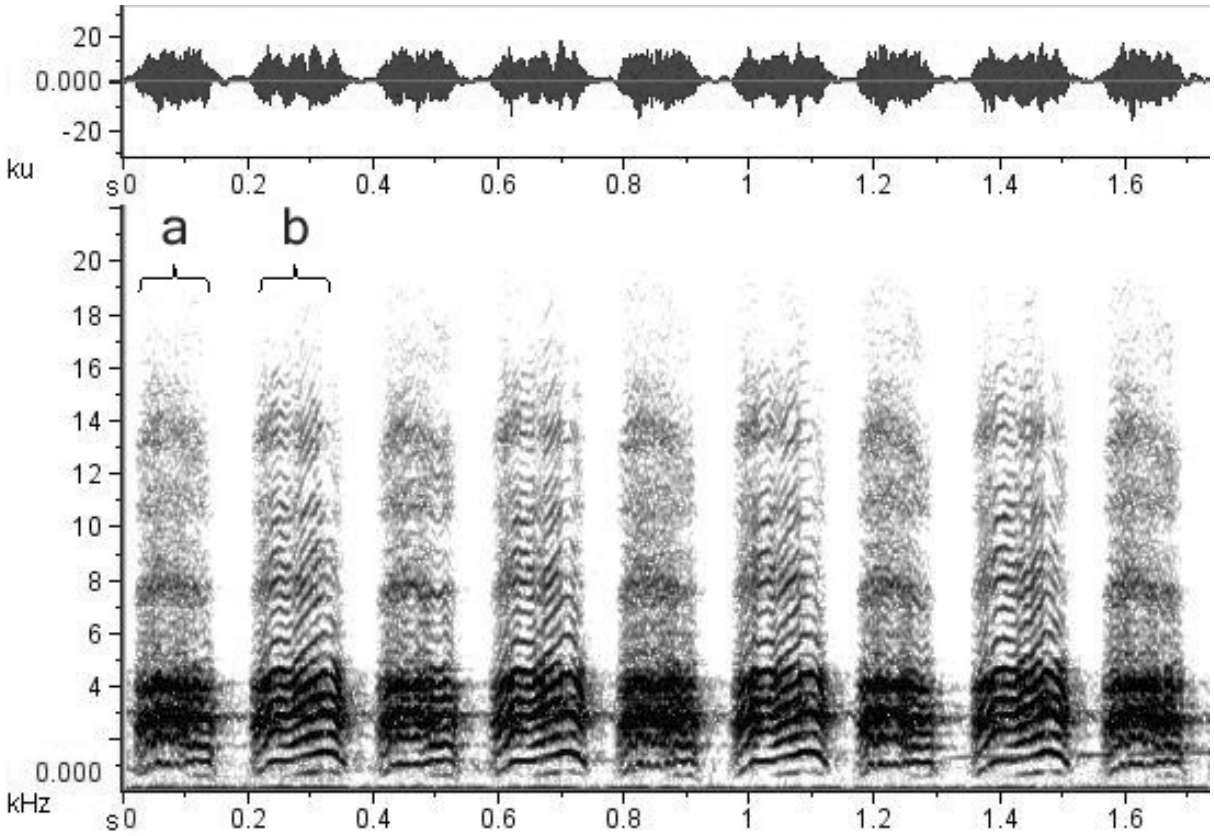
Figures

Fig. 1. Spectrogram and waveform views of the three loud call types, 1) the 'v shaped chatter', 2) the 'double note ascending chatter' and 3) the 'atonal chatter' as defined by Golabek (2010). For the double note ascending chatter, (a) denotes the 'small' syllable and (b) the 'long' syllable section of this call. Spectrogram windows are drawn in a Hamming window (512 point, with an overlap of 96.9%). Grey scale represents a 65db range.

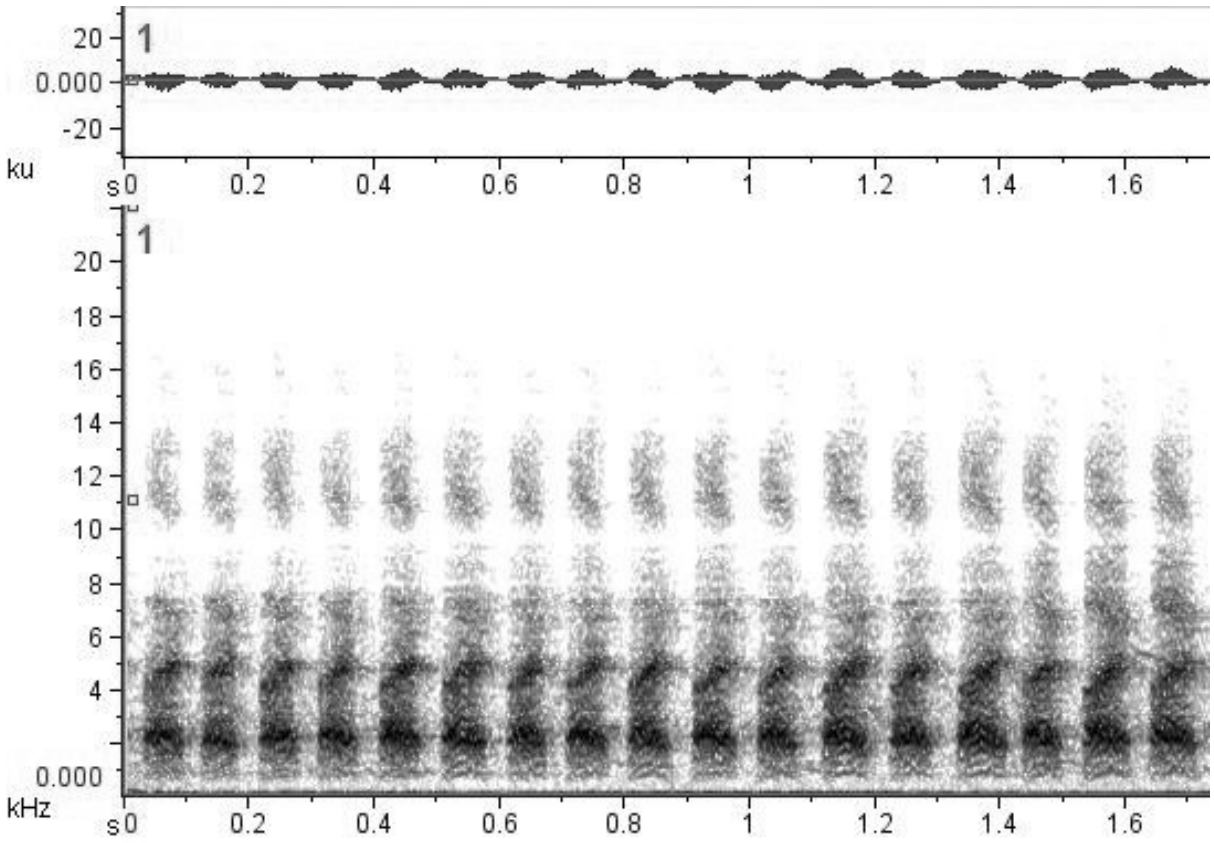
1) *the ' v-shaped chatter'*



2) *the 'double note ascending chatter'*



3) *the 'atonal chatter'*



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