

1 **Individually distinctive vocalization in Common Cuckoos**
2 **(*Cuculus canorus*)**

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5 **Sándor Zsebők¹, Csaba Moskát², Miklós Bán^{3*}**

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8 ¹Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös
9 University, H-1117 Budapest, Pázmány P. sétány 1/C., Budapest, Hungary

10 ²MTA-ELTE-MTM Ecology Research Group, Hungarian Academy of Sciences, a joint
11 research group of the Biological Institute of Eötvös Loránd University, Budapest, Pázmány
12 Péter sétány 1/C., H-1117 Budapest, Hungary and the Hungarian Natural History Museum,
13 Baross u. 13., Budapest, H-1088, Hungary

14 ³MTA-DE "Lendület" Behavioural Ecology Research Group, Department of Evolutionary
15 Zoology, University of Debrecen, Debrecen, H-4010, Hungary

16

17 *Corresponding Author: Miklós Bán, banm@vocs.unideb.hu

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26 **ABSTRACT**

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28 Distinctive individual vocalizations are advantageous in several social contexts. Both genetic
29 and environmental effects are responsible for this phenomenon resulting in different
30 frequencies and time domains of sounds in birds. This individuality can be utilized in
31 breeding bird censuses and abundance estimates. In this study we explored the individuality
32 of the advertisement calls of male Common Cuckoos (*Cuculus canorus*) with the aims of
33 describing the acoustic ways in which individuals differ from each other, and characterizing
34 the practical requirements for using statistical learning methods for individual recognition.
35 We collected calls from a Hungarian cuckoo population and conducted discriminant function
36 analysis on acoustic parameters to distinguish individuals. We show that individuals differ in
37 both the frequency and time of their calls, most importantly in maximum frequency of the
38 first syllable. Our discrimination of the male calls of 26 individuals was almost 100%
39 accurate, and even when the number of samples was reduced to five calls per individual, and
40 the number of acoustic parameters was decreased to five variables, accuracy still exceeds
41 90%. Thus, because our acoustic individual discriminaton technique is easy to perform and
42 can be readily automated, it will be applicable to a wide range of ecological and behavioural
43 studies.

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46 INTRODUCTION

47

48 Individuality in call characteristics can be adaptive in several communication contexts
49 (Lambrechts and Dhondt 1995; Tibbetts and Dale 2007), including parent-offspring
50 recognition in species with dense colonies (e.g., King Penguin *Aptenodytes patagonicus*;
51 Lengagne et al. 2001), or re-establishing pair-bonds in species with large colonies (e.g.,
52 Kittiwake *Rissa tridactyla*; Aubin et al. 2007; Blue-footed Booby *Sula nebouxii*;
53 Dentressangle et al. 2012). Unique calls are also advantageous for territorial species to enable
54 the recognition of neighbours (the ‘dear enemy theory’; Fisher 1954); this has been shown to
55 occur, for example, in Black Redstarts *Phoenicurus ochruros* (Draganoiu et al. 2014) and
56 Willow Warblers *Phylloscopus trochilus* (Jaska et al. 2015). Indeed, vocal individuality may
57 be especially advantageous in contexts where visual signals are unuseable, like in rainforests
58 (e.g., White-browed Warbler *Basileuterus leucoblepharus*; Aubin et al. 2004; Screaming Piha
59 *Lipaugus vociferans*; Fitzsimmons et al. 2008), in meadows where there is tall grass (e.g.,
60 Corncrake *Crex crex*; Rek and Osiejuk 2011), or birds that are active at night (e.g., Great
61 Horned Owl *Bubo virginianus*; Odom et al. 2013). Individually distinctive vocalization is
62 likely essential for long distance communication, as in the boom call of the Grey Crowned
63 Crane *Balearica regulorum gibbericeps* (Budde 2001) or the European Bittern *Botaurus*
64 *stellaris* (McGregor and Byle 1992).

65 Individual recognition in birds, however, depends on two conditions: (i) inter-individual
66 variation of the signaller’s vocalization has to be larger than the intra-individual variation, and
67 (ii) receivers must possess the ability to discriminate individuals (Tibbetts and Dale 2007).
68 The factors responsible for individually distinct vocalization include differences in anatomical
69 structures of the vocal organs and control of sound production (Ballintijn et al. 1995; Goller
70 and Riede 2013). Additionally, in some bird taxa (passerines, hummingbirds and parrots)
71 vocal individuality can also be developed, or modified, via learning, that has two main
72 sources: (i) social modification, and; (ii) learned acquisition (Boughman and Moss 2003).
73 Therefore individuals may differ both in time and frequency parameters (e.g., Aubin et al.
74 2004; Volodin et al. 2005), and in the composition of their signals (e.g., Kiefer et al. 2014).
75 From the viewpoint of the receiver, birds in general can perceive a change of less than 1%
76 pure tone frequency, and 10-20% difference in signal duration (Dooling 1982), while species
77 of oscine passerines possess elaborate cognitive capabilities even to discriminate syllable
78 sequences (Knudsen and Gentner 2010).

79 In this paper, we focus on the individual acoustic signals of the Common Cuckoo (*Cuculus*
80 *canorus*; hereafter "cuckoo"), a brood parasitic species distributed across the Palearctic region
81 and subdivided into several subspecies (Payne 2005). Cuckoos specialize on different host
82 species, so they are classified into 'host-specific races', or 'gentes'. These gentes show
83 differences in egg phenotypes, as these are adapted to resemble those of their hosts (i.e., egg
84 mimicry; Dawkins and Krebs 1979; Davies 2000). The advertising call of male cuckoos also
85 shows a highly stereotypical acoustic structure with two notes ("cu-coo") across their whole
86 distribution area (Lei et al. 2005; Wei et al. 2015), although quantitative features may vary by
87 health condition of individuals (Møller et al. 2016), between subspecies (Wei et al. 2015),
88 gentes, and populations (Fuisz and de Kort 2007), with increasing variation with geographic
89 distance (Wei et al. 2015). Regarding the taxonomic status of cuckoos we expect that cuckoos
90 do not learn their advertising calls (c.f. Catchpole and Slater 2008), but genetic and
91 environmental effects might generate individually distinctive call characteristics. Our interest
92 in studying cuckoo calls is two-fold: (i) to explore the biological aspect of acoustic
93 individuality, and; (ii) to apply this phenomenon to research and nature conservation.

94 The breeding behaviour of the Common Cuckoo suggests that individual discrimination
95 plays important role in intra-specific sexual selection. It is believed that male cuckoos are
96 territorial (Payne 2005), therefore it seems advantageous for them to discriminate between
97 their neighbours and intruders (the 'dear-enemy' theory, see above). Indeed, Lei et al. (2005)
98 worked with a much smaller sample (ten individuals) and suggested that male cuckoo
99 advertising calls show consistent inter-individual differences. Jung et al. (2014) later
100 examined nine individuals and also found that inter-individual variance in call parameters is
101 higher than within individuals and might thus be important for discrimination. However, these
102 previous hypotheses were not tested quantitatively using learning algorithms to see if
103 individual cuckoos really can be discriminated on the basis of their calls and how to do it in
104 practice.

105 More generally, there is emerging interest in the use of acoustic methods in
106 conservation (Laiolo 2010). Discrimination (distinguish individuals at a time) and
107 identification (recognize individuals on a longer time scale) based on acoustic features can
108 provide a non-invasive approach useful to different investigations (Terry et al. 2005). There
109 are examples of the use of such approaches for abundance estimates in Ortolan Buntings
110 *Emberiza hortulana* (Adi et al. 2010), censuses of European Bitterns and Black-throated
111 Divers *Gavia arctica* (Gilbert et al. 1994), Corncrakes (Peake and McGregor 2001; Budka

112 and Kokocinski 2015), and Woodcock *Scolopax rusticola* (Hoodless et al. 2008). These
113 methods are especially important in species where visual inspection is impaired like in dense
114 habitat or in animals active at night. Cuckoos are quite drab and timid birds, so the use of
115 color-tagged individuals for individual identification is challenging. Other techniques such as
116 ringing, individual tagging, and radio telemetry may cause disturbances (Sutherland et al.
117 2004). If a male advertising call can be heard from a distance, as for instance in cuckoos, it
118 offers a potential solution for acoustic identification of individuals that might help in studies
119 where we want to follow the individuals without any disturbance in observing their natural
120 behaviour.

121 In this study, we investigated acoustic individuality in the advertising calls of male
122 Common Cuckoos. Our main objectives were: (1) to describe the individually distinctive
123 parameters of these calls; (2) to test whether individuals can be discriminated by these
124 parameters; (3) to determine how sample size and number of measured acoustic parameters
125 affects the feasibility of using this method for a range of applications. To achieve these aims,
126 we recorded and analysed calls from a cuckoo population, applied Discriminant Function
127 Analysis (DFA) in a cross-validation framework, and interpreted the results from theoretical
128 and practical viewpoints.

129

130 **METHODS**

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132 **Study area and sound recording**

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134 This study was conducted in the surroundings of Apaj (47°07N; 19°060E), ca. 50 km south of
135 Budapest, Hungary, where the density of breeding Common Cuckoos is high and there is a ca.
136 50% parasitism rate (i.e. 50% of host nests contain at least one cuckoo egg; Zölei et al. 2015).
137 In this area, cuckoos are mainly distributed along linearly-structured irrigation channels where
138 trees are available for perching, and where these birds parasitize Great Reed Warbler
139 *Acrocephalus arundinaceus* clutches (Moskát and Honza 2000) (Fig. 1).

140 We recorded cuckoo sounds for five days between May 15th and 22nd, 2013, in the
141 mornings (6-11 h CET), and late afternoons (16-20 h CET), using a Telinga parabola dish
142 with a Sennheiser ME62 microphone and K6 preamplifier on a Tascam DR1 handheld digital
143 recorder (48 kHz sampling rate, 16 bit quality). We then later transferred recorded calls to a
144 PC for sound analysis (see below). Each cuckoo call was recorded from about a 20-30 m

145 distance, reasonable for this species and as done by Fuisz and de Kort (2007), and Wei et al.
146 (2015).

147 During the recording process we tried to record individual cuckoos just once by
148 sampling the whole area along channels, walking the banks in one direction only over a short
149 time (2-3 hours), while visually following the movement of birds. This meant that we met and
150 recorded just new cuckoos, but to avoid doubt we did not record when uncertain to avoid
151 duplicating data points. As we sampled each channel section just once within the study
152 period, and radio telemetry revealed that cuckoos stayed in relatively short sections along the
153 channels (typically < 1 km; our unpublished results; our unpublished results), we have a high
154 probability of confidence that we recorded each individual just once. The spatial distribution
155 of recorded individuals used for analyses is shown on the survey map of the area (Fig. 1).

156

157 **Sound analysis**

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159 Although a total of 29 individuals (3-11 individuals per day) were recorded, we present
160 recordings of just 26 birds with a minimum of 10 good quality calls (i.e., with low
161 background noise).

162 We then manually segmented the two syllables of each cuckoo calls (as done by Lei et
163 al. 2005; Fuisz and de Kort 2007; Jung et al. 2014; Wei et al. 2015), and measured each
164 syllable automatically in the following way: first, we searched for maximum syllable intensity
165 in the spectrogram, and then the start and end points each syllable were determined at a 20 dB
166 level lower than the maximum. Accordingly, we got comparable syllable parameters
167 independently of the absolute intensity of the calls and the background noise level (Zollinger
168 et al. 2012). The 20 dB limit was chosen, because at this level the characteristics of all
169 syllable shapes were explicit and at the same time they were above the actual background
170 level on all recordings.

171 In the next step, we measured several parameters of calls that characterize frequency
172 structure and time domain in a similar manner to previous studies (Lei et al. 2005; Fuisz and
173 de Kort 2007; Jung et al. 2014; Wei et al. 2015). Syllable frequencies were measured at the
174 starting point (i.e., $F1_{\text{start}}$ in the first syllable, and $F2_{\text{start}}$ in the second syllable), at the end (i.e.,
175 $F1_{\text{end}}$ and $F2_{\text{end}}$) of each syllable, and at maximum frequency ($F1_{\text{max}}$ and $F2_{\text{max}}$). The length of
176 both syllables ($T1$ and $T2$), and the pause (T_{pause}) between the two syllables in the call, were
177 also measured. We found four highly correlating ($r > 0.7$) such pairs of parameters.

178 Based on these nine basic measurements, we derived a series of new variables based
 179 on their differences (Fig. 2); because we expect lower correlations between these new
 180 variables than when absolute frequencies are used, our approach is more effective in
 181 characterizing the shape of syllables. Although a similar approach was used by Fuisz and de
 182 Kort (2007), we derived five new parameters in this study, retaining four basic variables from
 183 the earlier study (Fuisz and de Kort 2007). Relative starting frequency of syllables was
 184 calculated as the difference between maximum frequency and starting frequency (i.e., $\Delta F1_{start}$
 185 $= F1_{start} - F1_{max}$ for the first syllable, and $\Delta F2_{start} = F2_{start} - F2_{max}$ for the second syllable). The
 186 relative ending frequency ($\Delta F1_{end}$ and $\Delta F2_{end}$) was taken as the difference between the ending
 187 frequency and starting frequency ($\Delta F1_{end} = F1_{end} - F1_{start}$ and $\Delta F2_{end} = F2_{end} - F2_{start}$). We used
 188 the absolute frequency measurement for the first syllable ($F1_{max}$) and a relative measurement
 189 for the second syllable ($\Delta F2_{max} = F2_{max} - F1_{max}$) to characterize the maximum frequency in
 190 each syllable. Beside of these six frequency parameters we used the T1, T2 and T_{pause} time
 191 parameters to describe the characteristics of cuckoo calls, altogether resulting in nine
 192 parameters used in subsequent analyses (Fig. 2), where we found no highly correlating pairs
 193 of parameters.

194 All measurements were taken using 2048 point-length FFT and Hann window with
 195 98% overlap while syllable segmenting and all acoustic analyses were conducted with the
 196 help of self-written scripts in the Matlab 2013 (The MathWorks Inc.) environment using the
 197 Signal Processing Toolbox (Version 6.19).

198

199 **Statistical analyses**

200

201 In order to choose the most appropriate variables for sound classification, we calculated the
 202 intra-individual and between-individual coefficients of variations in each parameter using the
 203 formula $CV = 100 * (1 + 1 / (4 * n)) * SD / \text{mean}$, where n is sample size and SD is standard
 204 deviation (Sherrer 1984; Sokal and Rohlf 1995). For the intra-individual coefficient of
 205 variation (CV_i), we computed CV for each individual based on all calls belonging to an
 206 individual and then calculated the mean of all CVs; for the between-individual coefficient of
 207 variation (CV_b), we used the mean parameter value from all individuals. The ratio of CV_b/CV_i
 208 is the measure of Potential Individual Coding ("PIC", Charrier et al. 2001; Mathevon et al.
 209 2003; Favaro et al. 2015), which shows the importance of a given parameter. We decided to
 210 involve a parameter in the classification procedure if its PIC value was greater than 1. This

211 means that the inter-individual variation is higher than the intra-individual variation expressed
212 by this parameter, suggesting that the actual parameter can be used for detecting individuality
213 (Charrier et al. 2001). Based on this criterion, just $\Delta F1_{\text{end}}$ and $\Delta F2_{\text{start}}$ were excluded, so
214 therefore we used seven out of the nine variables for classification. To evaluate these seven
215 variables, we conducted a linear Discriminant Function Analysis (DFA) for 10 randomly
216 chosen calls for each individual, and then calculated the Bartlett's approximate chi-squared
217 statistic to test the canonical correlation coefficients.

218 For classification of calls in the first step, 10 calls were randomly chosen for each
219 individual, and then two different classification procedures were used: a one-call
220 classification, and a multi-call classification.

221 For the one-call classification, following a 10-fold cross-validation procedure (Stone
222 1974), we divided data into a training dataset with nine calls and test dataset with one call
223 from each individual in each round. We used DFA on the training dataset to classify calls, and
224 then the DFA model was applied to the test dataset. After 10 cycles of the 10-fold cross-
225 validation, we repeated the whole process using a randomly sampled set of 10 calls from the
226 pool of calls for each individual. After 100 repetitions of cross-validation, we summarized the
227 results in a contingency table (called a confusion matrix) representing the class predictions
228 with respect to the actual outcome, and calculated the mean percent of true positive cases.

229 In the multi-call classification we divided the 10 calls of an individual into five
230 training and five test calls. Then, similarly to the one-call classification, we taught and then
231 tested the DFA model, repeating these steps 10 times. In each cycle, we assigned calls to the
232 individual bird that had more classified calls, and repeated the whole cross-validation process
233 100 times, using randomly sampled 10 calls from the pool of calls of each individual. We
234 calculated the results in the same way to the one-call classification.

235 In the next step we studied how the sizes of the training and testing datasets influence
236 our classification results both in the one-call and multi-call cases. In each round we chose
237 randomly two to five calls from the training dataset from each individual to train the DFA
238 model, and one to five calls from the testing dataset to validate the model. We repeated the
239 whole process 100 times, and calculated the accuracy for all possible pairwise combinations
240 of the training and testing samples.

241 We also computed the accuracy of one-call and multi-call classifications, based on the
242 different number of variables. These were ordered increasingly, based on their PIC value, and
243 in each step we increased the number of variables by one in the DFA model. This means that

244 in the one-variable model only the variable with the highest PIC value was included, but in
245 the seven-variable model all seven original variables were used. We plotted the classification
246 accuracy against the increasing number of variables.

247 All statistical analyses were carried out in MATLAB 2013, using the Statistical
248 Toolbox (Version 8.2) and the RAFISHER2CDA Canonical Discriminant Analysis Toolbox
249 (Trujillo-Ortiz et al 2004).

250

251

252 **RESULTS**

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254 We analysed 1489 calls related to 26 individuals (57.3 ± 39.9 in mean \pm SD calls per
255 individual) for subsequent analyses. In general, the first syllable of the call has a reversed U-
256 shape frequency contour between 600 and 750 Hz, while the second syllable has a quasi-
257 constant frequency in the range 500-600 Hz. These two syllables, including a short pause
258 between them, covers an about 0.17 second period (Table 1). The calls were repeated
259 regularly (1.34 ± 0.17 calls/min in mean \pm SD).

260 By visual inspection of spectrograms, the intra-individual variability of call structure
261 appears to be less than inter-individual variability, but both the shape and peak frequencies
262 show considerable differences (Fig. 3). For seven variables ($F1_{\max}$, $\Delta F2_{\max}$, $\Delta F2_{\text{end}}$, T_{pause} , $T2$,
263 $T1$, $\Delta F1_{\text{start}}$) the PIC was higher than 1 (Table 1). The parameter with the highest PIC value
264 was $F1_{\max}$, suggesting that this parameter contributes most to individually distinctive
265 vocalization, and thus may play a key role in the classification of individuals. In the DFA, all
266 seven canonical variables proved to be significant, therefore we retained them in the model
267 (χ^2 -test, $p < 0.001$ for all canonical roots).

268 Our cross-validation procedure of one-call classification had a 92% accuracy using the
269 seven chosen variables (Fig. 4A), while our multi-call classification was 98% accurate (Fig.
270 4B). We also reveal the role of sample size in the training and testing procedure: In the one-
271 call classification, we found that by using two calls as a minimum to train, and one call to test
272 the model was adequate to 82% accuracy; and with at least four calls to train and two calls to
273 test the model we achieved over 90% accuracy (Fig. 4C). The multi-call classification gave
274 better results than one-call classification with minimum accuracy of 96% when using a
275 minimum of three calls both to train and test the model (Fig. 4D).

276 We also investigated the importance of the number of variables used in the
277 classification procedure: Accuracy of classification increased with increasing number of
278 variables, higher in the multi-call classification than in the one-call classification (Fig. 5)
279 across all variables. We found the largest jump in saturation curves between the cases when
280 one and two variables were used in the models; using just five variables, the one-call
281 classification yields more than 80% accuracy on average (CI: 76.9-87.3 %), while the multi-
282 call classification model reaches 95% accuracy on average (CI: 80.8-100%). When we
283 randomly allocate calls to individuals, accuracy is just 3.85% and demonstrates the
284 effectiveness of the use of DFA for classification.

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286

287 **DISCUSSION**

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289 In general, we found that male cuckoos use individually distinct advertisement calls that can
290 be unambiguously discriminated by DFA classification. Overall frequency and time
291 parameters show a large degree of agreement with previous studies, supporting the idea that
292 the male's advertisement call in this species is highly consistent throughout its distribution
293 area (Lei et al. 2005; Jung et al. 2014; Wei et al. 2015).

294 We found that individuality is encoded in both frequency and time domain. In this
295 cuckoo species, in accordance with our study, both Lei et al. (2005) and Jung et al. (2014)
296 found that the frequency and time parameters of advertisement calls are individually
297 distinctive. This multi-parametric individual coding is generally found in acoustic bird studies
298 resulting in diverse solutions for conveying safe signal transfer in the acoustic space.
299 Individuality might be coded by frequency modulation and signal duration as in the King
300 Penguin (Lengagne et al. 2001), or by frequency gaps between the signal components and
301 their positions as in the White-browed Warbler (Aubin et al. 2004). However, in the
302 Corncrake (Budka and Osiejuk 2013) individuality seems to be encoded by pulse-to-pulse
303 duration, while in the Blue-footed Booby, males are mainly time-coded, but females are
304 frequency coded individually, two different solutions for acoustic individual recognition in
305 large and noisy breeding colonies (Dentressangle et al. 2012).

306 The highest frequency ($F1_{\max}$) of the first syllable is the most important parameter we
307 found in the individual discrimination (i.e. with the highest PIC value). Interestingly, this
308 parameter seems to have less importance in causing habitat and population differences: Fuisz

309 and de Kort (2007) suggested that cuckoos from different habitats and/or different genes
310 mostly differ in the absolute frequency parameters of the second syllable. Wei et al (2015)
311 found differences in the bandwidth of the second syllable that can be attributed to habitat,
312 while population differences are best explained by the lowest frequency of the first syllable,
313 the frequency band of the second syllable, and time parameters (Fuisz and de Kort 2007). Our
314 results suggest that individual differences are mainly coded in the highest frequency parts of
315 the first syllable, and so generate high inter-individual variation in a population.
316 Consequently, inter-population and inter-gens differences are not expressed in the highest
317 frequency of the first syllable of the "cu-coo" calls.

318 We found that the seven acoustic parameters allowed nearly perfect individual
319 discrimination of cuckoos, especially when several calls from a calling sequence were used.
320 Indeed, even using less variables this method might be feasible, as with five variables the
321 classification accuracy still reached 90%. From a practical point of view, five out of seven
322 variables ($F1_{\max}$, $\Delta F2_{\max}$, T_{pause} , T2, T1) are reasonably easy to extract using automatic
323 segmenting and measuring (e.g. with the programs Avisoft SASLab Pro or Raven Pro).
324 Consequently, the whole discrimination process can readily be automated which may help the
325 use of this simple method for the discrimination of cuckoo individuals in a population. We
326 show that three calls from a male could be adequate both to teach the statistical model and test
327 it later to reach a 90% level of accuracy; this seems an attainable amount of sound samples
328 from individual cuckoos in the field.

329 Theoretically, we cannot exclude the case when a high number of cuckoos are
330 presented in a small area, making individual discrimination more difficult. However, the
331 density of cuckoos in the breeding season cannot reach extremely high values because of their
332 need for host nests for reproduction, and the availability of suitable nests limits brood
333 parasites' density. This statement is also valid for our site where parasitism rate of Common
334 Cuckoos seems to be permanently the highest in the world. About 50-64% of Great Reed
335 Warbler clutches are parasitized here (Zölei et al. 2015), where the Great Reed Warbler was
336 found to be the only host species currently parasitized. We believe that if our method of
337 cuckoos' discrimination by sound works here, this method should also work at lower cuckoo
338 densities.

339 Cuckoo males frequently use their advertising calls in the breeding season (Payne
340 2005), therefore in this period it seems feasible to apply the acoustic method for census and
341 abundance estimation similarly to studies used in other species (Gilbert et al. 1994; Peake and

342 McGregor 2001; Hoodless et al. 2008; Adi et al. 2010; Budka and Kokocinski 2015). To use
343 an acoustic method for individual tracking over a longer period, however, additional
344 examination is needed to reveal how a given signal changes with time (Mennill 2011). In this
345 case, the task is not only to discriminate the individuals, but also to identify them. Several
346 studies have already focused on this question, for example in Corncrakes (Budka et al. 2015),
347 European Eagle Owls *Bubo bubo* (Grava et al. 2008), European Bitterns, Black-throated
348 Divers (Gilbert et al. 1994), and Mexican Ant-thrushes *Formicarius moniliger* (Kirschel et al.
349 2011). Individually distinct vocalization can also be used for the estimation of survival and
350 population responses (Pollard et al. 2010). The fundamental frequency of acoustic signals
351 depends not only on the anatomical structures of the syrinx, but also on the operation of the
352 syringeal muscles and air sac pressure (Goller and Riede 2013) under neural control. For this
353 reason, the general physiological state of the individual, hormonal status, and social context
354 may influence advertisement call characteristics, as in the song of the Zebra Finch
355 *Taeniopygia guttata*, where fundamental frequency is influenced by the food availability
356 (Ritschard and Brumm 2012). We argue that further studies could clarify how intra-individual
357 acoustic signals change over time, as well as how the social structure of cuckoos may affect
358 the acoustic parameters of individuals. Also, further experimental studies are needed to test if
359 cuckoos are able to discriminate each other by sound and use this information in their decision
360 making regarding territoriality and in their social behaviour.

361

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363

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371

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499 Table 1. Statistical summary of acoustic variables of Common Cuckoo calls. The parameters
 500 are ordered in decreasing importance, according to their decreasing PIC value. “Mean” is the
 501 average of individuals’ mean values; “SD” is the standard deviation of individuals’ mean
 502 values, “min ; max” are the minimum and maximum of individuals’ mean values, “CVi” is
 503 the intra-individual coefficient of variation, “CVb” is the between-individual coefficient of
 504 variation.

505

	mean	SD	min ; max	CVi	CVb	PIC
F1_{max} (Hz)	676	28	617 ; 748	1.4	4.2	2.97
ΔF2_{max} (Hz)	-136	16	-164 ; -114	6.3	12.2	1.94
ΔF2_{end} (Hz)	4	10	-20 ; 19	150.6	277.3	1.84
T_{pause} (s)	0.179	0.015	0.152 ; 0.204	5	8.5	1.69
T1 (s)	0.097	0.009	0.078 ; 0.129	5.8	9.6	1.67
T2 (s)	0.160	0.016	0.128 ; 0.197	6.2	10	1.62
ΔF1_{start} (Hz)	-112	24	-183 ; -61	20.1	21.4	1.07
ΔF2_{start} (Hz)	-23	8	-38 ; -4	48.3	34.3	0.71
ΔF1_{end} (Hz)	-9	18	-49 ; 29	562.7	208.2	0.37

506

507 Legend to figures

508

509

510 FIGURE 1. Map of the sampling area. The localities of the 29 recordings are marked with
511 dots on the map.

512

513 FIGURE 2. Measured and derived call parameters used in the analyses

514

515 FIGURE 3. Sample sonograms of the "cu-coo" calls from 5 individuals with 5 samples each.

516

517 FIGURE 4. The results of DFA classification. (A) Confusion matrix of one-call classification,
518 (B) confusion matrix of multi-call classification. The hitmaps of the confusion matrices show
519 the percentages of the correct classification in the main diagonal. (C) and (D) DFA
520 classification using different number of train and test calls in the model. The hitmaps show
521 sample size dependency of the classification accuracy in one-call classification (C) and multi-
522 call classification (D).

523

524 FIGURE 5. The result of the DFA classification using different number of variables. The plot
525 shows the effect of the number of variables used in DFA. The variables were put into the
526 models with their decreasing PIC values.

527

528

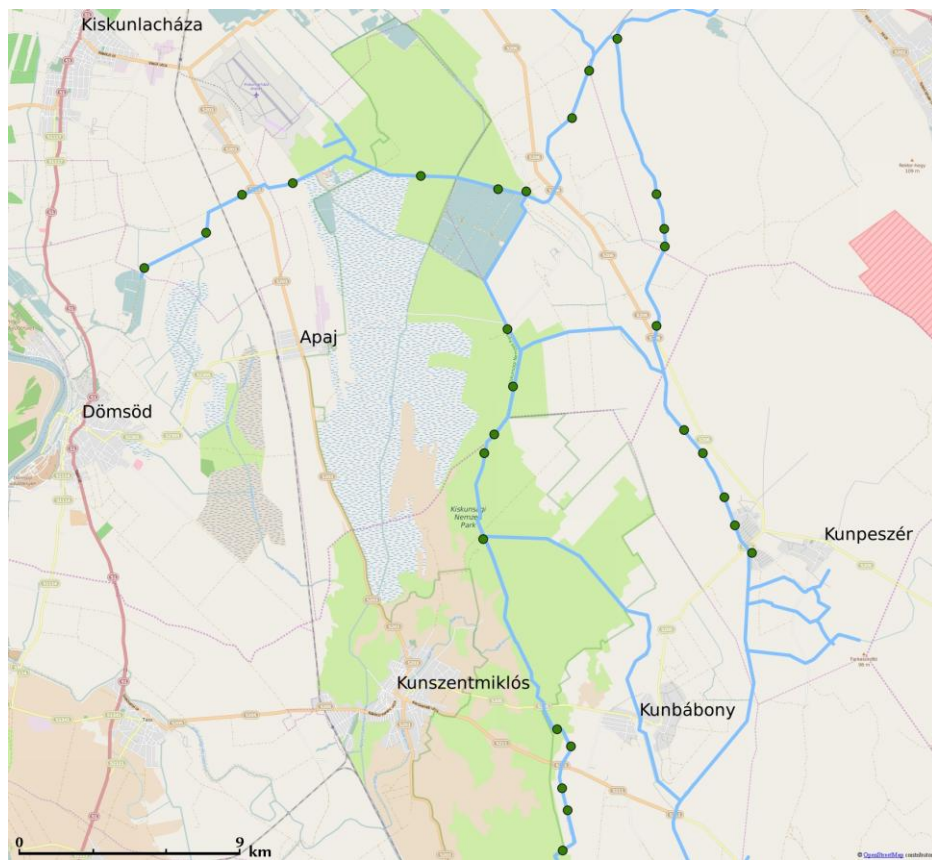
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532 Figure 1

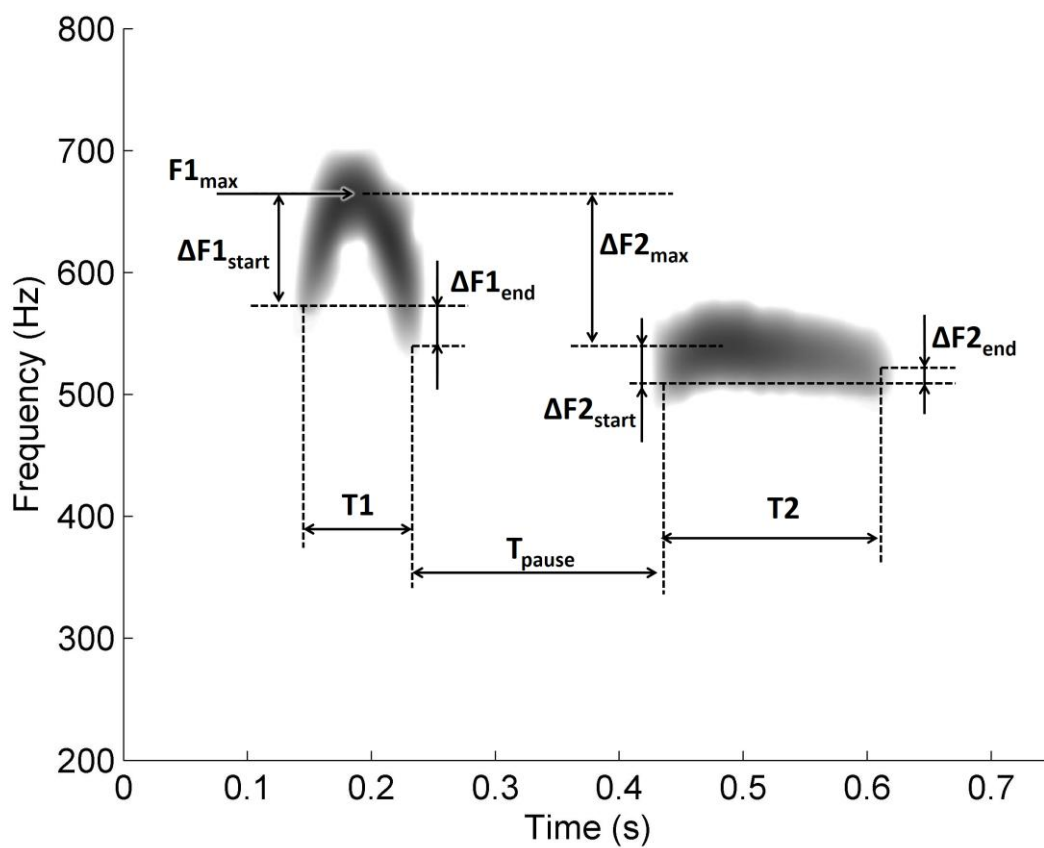
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536 Figure 2



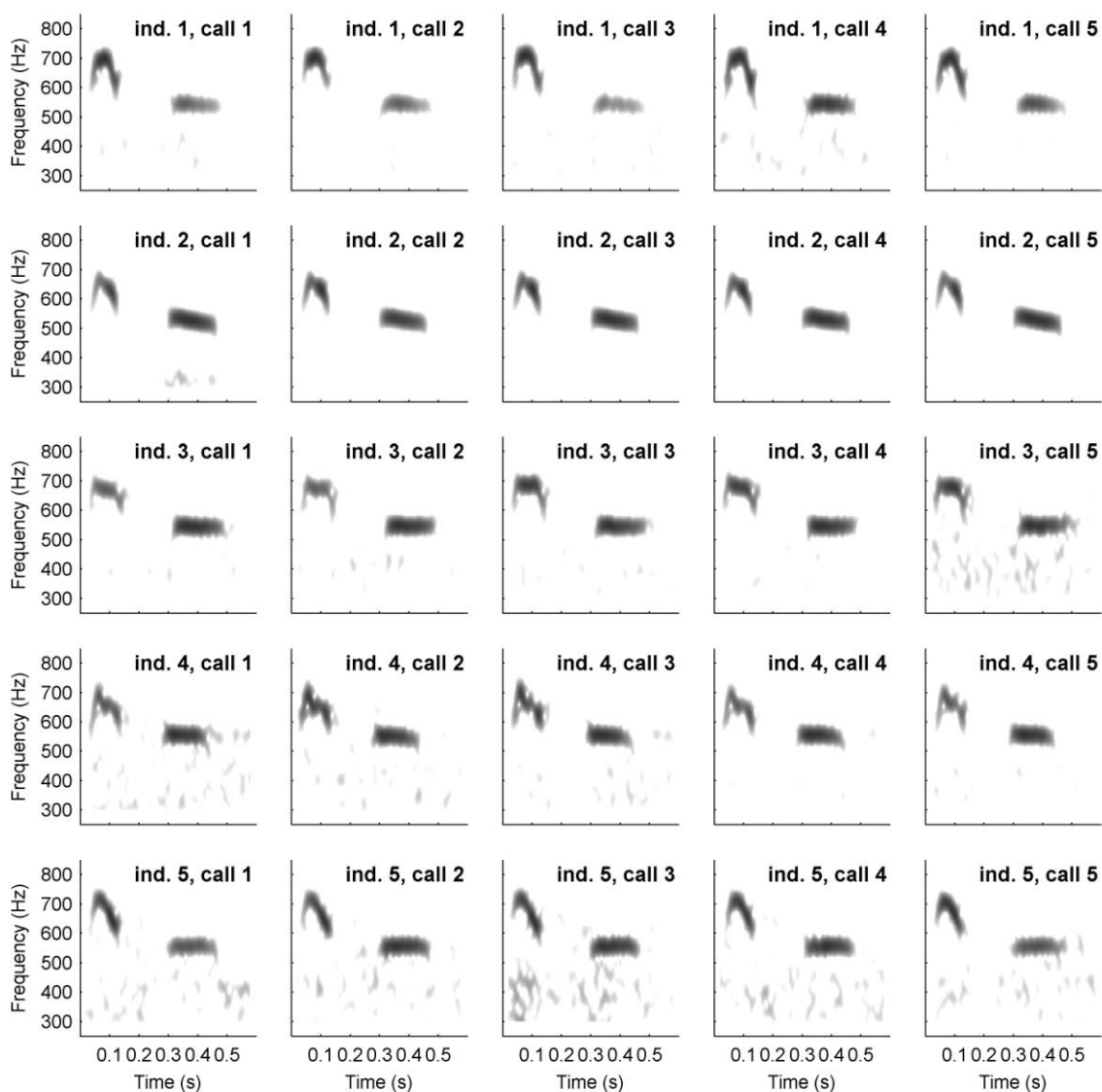
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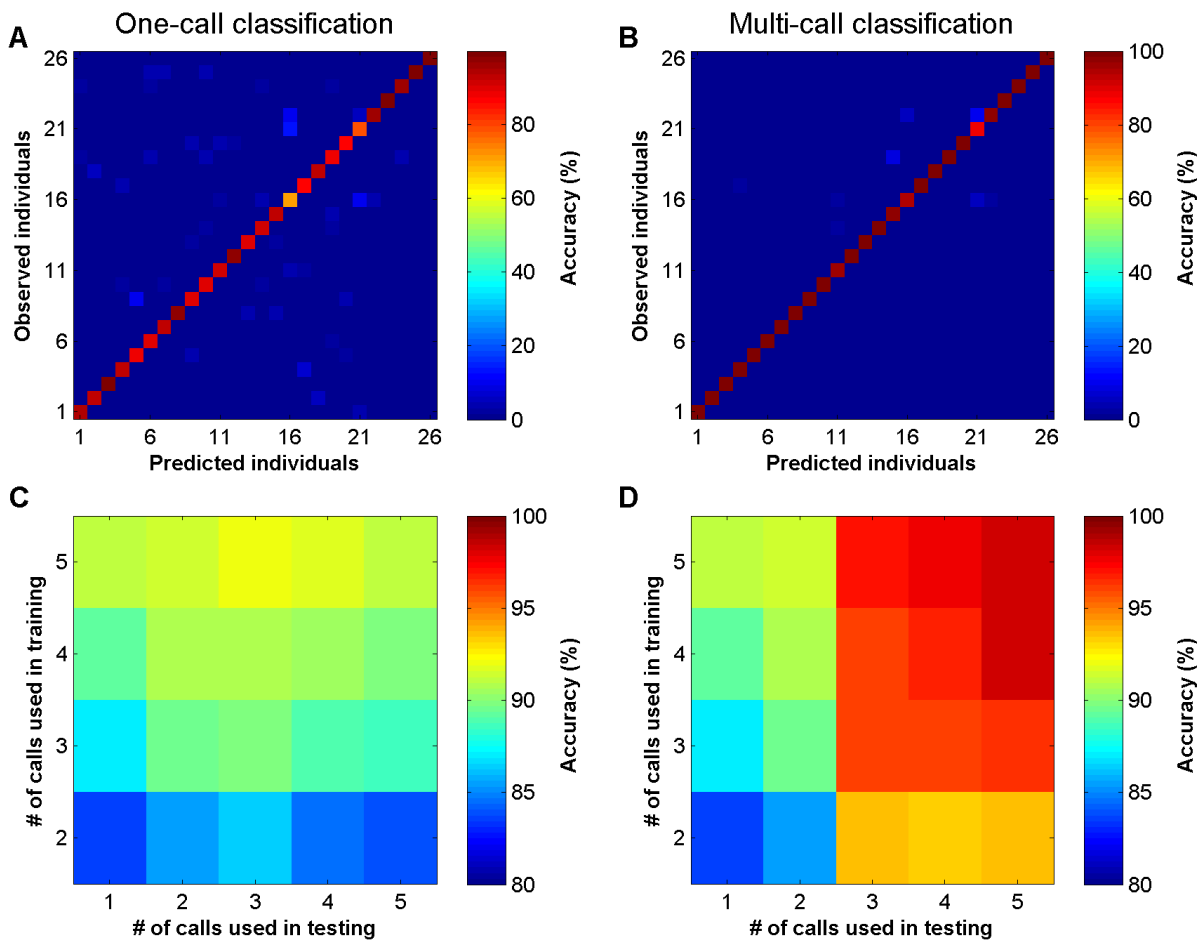
541 Figure 3



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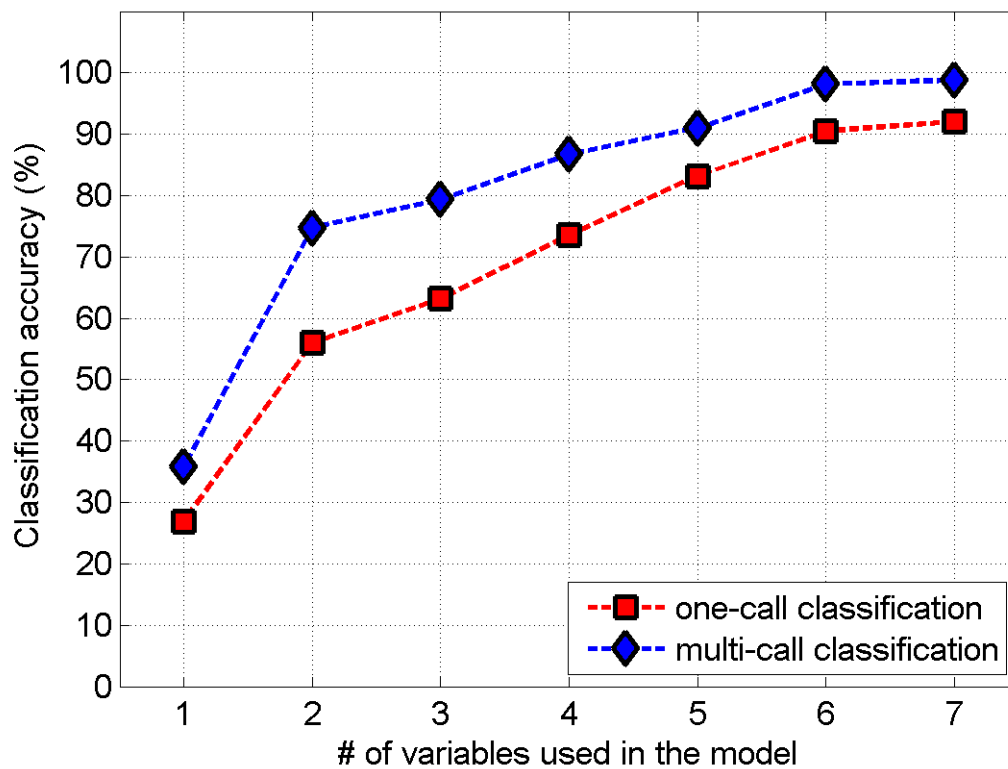
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544 Figure 4



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546 Figure 5



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