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1 **Shared Calls in Repertoires of Two Locally Distant Grey Parrots (*Psittacus erithacus*)**

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27

## 28 **Abstract**

29 Parrots belong to the handful of animal species capable of vocal production learning. They are  
30 considered to be open-ended learners with complex and variable vocalizations. It is not  
31 known, however, to what extent their repertoires are shared among individuals within a group  
32 or between vocally isolated individuals or groups. In Study 1, we mapped the repertoire of  
33 four captive African grey parrots (*Psittacus erithacus*) using a combination of three acoustic  
34 analyses. In Study 2, we compared the repertoire of two female African grey parrots from two  
35 different laboratories who had never been in vocal contact with each other or any member of  
36 the other parrot's social group. Results of Study 1 showed a relatively large agreement  
37 between all three methods used to analyze the vocalizations. Almost three quarters (72.8%) of  
38 categories determined by visual-acoustic analysis were confirmed by at least one of the two  
39 computer-aided methods used, i.e., by spectrographic cross-correlation and/or a  
40 multiparametric statistical method. In Study 2, we found a relatively large proportion of calls  
41 shared between the repertoires of the two grey parrot subjects. Over half and over a fourth of  
42 calls produced by parrots with the smaller and the larger repertoire, respectively, were shared  
43 between the two. No previous study identified such a large proportion of intergroup shared  
44 calls within this parrot species. It seems that some calls tend to reappear in vocally isolated  
45 groups based on inherited predispositions, similarly as has been documented in songbirds.

46 **Keywords:** vocal learning; African grey parrot; vocalization; spectrographic cross-correlation

47 **Introduction**

48 Social vocal production learning, which takes place when individuals modify their  
49 vocalizations by imitating others (Janik and Slater 2000), requires complex neural adaptations  
50 (Jarvis 2004) and is considered relatively rare. So far, it has been identified only in a few  
51 mammalian species, including humans, cetaceans, pinnipeds, bats, and elephants (Jarvis 2004;  
52 Janik 2014; Reichmuth and Casey 2014; Knörnschild 2014; Stoeger and Manger 2014), and in  
53 three groups of birds, namely songbirds, hummingbirds, and parrots (Brainard and Doupe  
54 2002; Mooney 2009; Araya-Salas and Wright 2013; Pepperberg 2010).

55 Unlike songbirds, practically all parrot species are considered open-ended vocal learners  
56 (Bradbury 2003; Dahlin et al. 2014), which means they have the ability to modify their  
57 repertoires even in adulthood (Todt and Geberzahn 2003). Their vocal repertoires are highly  
58 complex and variable (Bradbury 2003), which is probably why parrots so far received less  
59 attention than songbirds in terms of repertoire mapping. Nevertheless, there are several  
60 studies on the vocal repertoire of parrot species such as budgerigars (Brittan-Powell et al.  
61 1997; Hall et al. 1997), lilac-crowned amazons (Montes-Medina et al. 2016), keas (Schwing  
62 et al. 2012), orange-fronted parakeets (Bradbury et al. 2001), and yellow-faced parrots (De  
63 Araújo et al. 2011).

64 Among parrots, the African grey parrot (*Psittacus erithacus*) is a species universally known  
65 for its outstanding ability to mimic both animate vocalizations and inanimate sounds  
66 (Cruickshank et al. 1993; Pepperberg, 1999). It has been demonstrated that they can learn to  
67 imitate human vocalizations and acquire some understanding of the concepts related to human  
68 words. Specifically, using the Model/Rival (M/R) technique based on imitation of speech  
69 between two humans by a parrot motivated to take part in the interaction, grey parrot Alex

70 learned to label numerous objects, quantities, materials, shapes, and colors, and to use the  
71 concept of the same and different (Pepperberg 1999, 2002, 2010).

72 Social learning of vocalizations in semi-natural conditions has been studied in budgerigars  
73 (e.g. Hile and Striedter 2000; Hile et al. 2000) and parrotlets (e.g. Berg et al. 2012; Wanker et  
74 al. 2005), whose vocal repertoire is, however, significantly narrower than that of grey parrots.  
75 One should not, therefore, generalize the findings of these studies to parrot species with rich  
76 vocalization repertoires.

77 The vocal repertoire of grey parrots has been studied both in captive individuals and in the  
78 wild (Cruickshank et al. 1993; Giret et al. 2012; May 2004) with variable results.  
79 Comparisons between repertoires of grey parrot groups are scarce and existing studies offer  
80 no conclusions regarding the extent to which repertoires are shared or unique to individuals or  
81 groups. Cruickshank described 88 call types in a wild grey parrot pair, including nine call  
82 types of other bird species and one bat call. May (2004) found 39 acoustic call types sorted in  
83 four classes in wild grey parrots, while Giret et al. (2012) distinguished 168 different grey  
84 parrot calls in their captive group, 30 of which were imitations of French labels. These authors  
85 also noted it was difficult to find calls shared between captive parrots and parrots in the wild  
86 and suggested that most grey parrot call types are learned. Begging calls, used shortly after  
87 hatching to indicate distress and elicit allofeeding, seem to be the only calls considered clearly  
88 innate (Hall et al. 1997).

89 While literature is far from unanimous with respect to the composition and size of grey  
90 parrots' vocal repertoire, our knowledge of the role of social environment in its development  
91 is even more limited. To improve our understanding of these subjects, in the first study  
92 reported here we tried to describe the vocal repertoire of this species. In the second study, we  
93 compared the repertoires of two locally distant individuals to arrive at a rough estimate of

94 similarity between repertoires of locally distant grey parrot groups. We worked with a group  
95 of four captive African grey parrots and one other captive grey parrot who never had any  
96 contact with this small group. We established the repertoire of all four captive grey parrots  
97 using a combination of three acoustic analyses and compared the repertoire of one female  
98 parrot from this small group with the repertoire of a female grey parrot from a different  
99 laboratory. Identification of shared calls in the repertoires of these two females who had no  
100 contact could serve as an argument for the existence of calls allegedly produced by all grey  
101 parrots, possibly based on some innate component. A comparison of proportions of shared  
102 inter- and intra-group calls could be the first step towards assessing the role of social learning  
103 versus innate predispositions in the establishment of repertoire in this species.

#### 104 **Study 1: Repertoire mapping**

105 In agreement with previous studies (e.g. May 2004, Giret 2012), we assumed that grey parrots'  
106 calls can be classified into discrete categories. The vocal repertoire of a species is mapped by  
107 visual-acoustic inspection of spectrograms by human categorizers (Janik 1999; Bloomfield et  
108 al. 2005). The main disadvantage of this approach is that the threshold values for categorizing  
109 vocalizations are not clearly defined (Janik 1999). Moreover, humans might well miss  
110 differences of importance to the animals and more generally, classification by human  
111 categorizers is inevitably biased by subjective perception. The biological meaning of majority  
112 of grey parrots' calls is unknown and moreover, it is uncertain to what extent grey parrots'  
113 acoustic perception and spontaneous tendency to categorize calls is similar to human acoustic  
114 perception and categorization. Nevertheless, it has been argued that the acoustic systems of  
115 parrots and humans are largely analogical (e.g. Bottoni et al. 2009; Patterson and Pepperberg  
116 1998; Pepperberg 2010) (see also discussion). The presence of multiple categorizers,  
117 proposed by Janik (1999), may reduce the inherent subjectivity but inter-categorizer reliability  
118 could be influenced by several factors (Jones et al. 2001). For these reasons, several

119 computer-aided methods had also been recently applied to the mapping of animal vocal  
120 repertoire.

121 The first commonly used computer-aided approach is spectrographic cross-correlation method  
122 developed by Clark et al. (1987). Spectrographic cross-correlation produces a similarity  
123 matrix between pairs of signals in a database. Similarity is measured as the peak of correlation  
124 between spectrograms of two calls by sliding two spectrograms across one another on the time  
125 axis. Each pixel in one spectrogram is compared with the corresponding pixel in the second  
126 spectrogram and time shift between the two is gradually modified until the point of maximum  
127 similarity is determined and measured, which creates a correlation matrix (Clark et al. 1987;  
128 Charif et al. 2010). This process is not affected by subjective perceptions of human  
129 categorizers and moreover, instead of focusing on particular sound parameters, it compares  
130 the entire spectrogram visualizations of calls (Khanna et al. 1997). It does, however, suffer  
131 from other limitations. The main problem is that correlation values are sensitive to fast  
132 Fourier transform frame length used for spectrogram generation (Baker and Logue 2003;  
133 Cortopassi and Bradbury 2000; Khanna et al. 1997). Moreover, the efficiency of this method  
134 decreases with increasing background noise in the recorded calls (Cortopassi and Bradbury  
135 2000; Khanna et al. 1997) and the method fails to detect small differences in the sound  
136 structure that could be significant (Khanna et al. 1997). And even more importantly, the  
137 abovementioned studies tested the efficiency of spectrographic cross-correlation on tonal or  
138 harmonic calls but sounds with atonal qualities were not tested. This method's performance  
139 with respect to atonal sounds is thus yet to be examined.

140 Another commonly used computer-aided approach is based on extracting parameters directly  
141 from the calls (e.g. amplitude, call duration, energy distribution, frequency bandwidth). These  
142 parameters typically represent mathematically well-defined frequency and temporal  
143 characteristics of the call. This method's main advantage is that it avoids categorizer's

144 subjectivity and it can be highly accurate (e.g. Pérez-Espinosa et al. 2015; Tchernichovski et  
145 al. 2000). On the other hand, it is limited by the range of feature sets used, which need not be  
146 applicable to a particular categorization (Giret et al. 2011). Parameters are extracted either  
147 manually or automatically using various commercial sound programs such as Avisoft-  
148 SASLab Pro [Raimund Specht, Berlin] or Raven Pro [Cornell Lab of Ornithology] custom  
149 programs such as the LMA, which focus on atonal sounds (developed by K. Hammerschmidt;  
150 see Schrader and Hammerschmidt 1997), or Sound-analysis R packages, such as Seewave  
151 (Sueur et al. 2008), EchoviewR (Harrison et al. 2015), or warbleR (Araya-Salas and Smith-  
152 Vidaurre 2017). Extracted parameters are then processed using a discriminant function  
153 analysis. This method has been applied to several vocal studies of primates (Hedwig et al.  
154 2014; Fischer et al. 2001; Pfefferle et al. 2016; Price et al. 2014), horses (Policht et al. 2011),  
155 rhinos (Policht et al. 2008), humans (Jürgens et al. 2011), passerine birds (Naguib et al. 2001),  
156 and cockatoos (Zdenek et al. 2015) and proved to be highly useful. In the following, we call it  
157 the multiparametric statistical method.

158 Aside from these commonly used methods, Giret et al. (2011) proposed an approach known  
159 as feature generation method. This classification method combines human categorizers'  
160 involvement with automatic feature measurement. In particular, visual categorization is used  
161 as a training database subsequently used to train and test a classifier by a supervised  
162 classification technique (Giret et al. 2011). Feature generation outperforms methods based on  
163 standard features in studies on animal vocalization (Giret et al. 2011; Larranaga et al. 2015;  
164 Molnár et al. 2008). On the other hand, due to its poor performance on full repertoires, it has  
165 only been applied to a limited number of call types. Giret et al. (2011) suggest that the best  
166 approach is to combine the complex integrating capability of the human eye with the  
167 objective specificity of an automatic process.



168 In Study 1, we classified vocalizations of four captive bred grey parrots (*Psittacus erithacus*)  
169 from a Czech laboratory using visual-acoustic classification by human categorizers.  
170 Categorization determined by the visual-acoustic method provided the foundation for its  
171 verification by two computer-aided methods: (1) a comparison of cross-correlation  
172 coefficients and (2) a multiparametric statistical method using the discriminant function in  
173 statistical analysis. We expected the cross-correlation method to perform better in the  
174 classification of tonal and harmonic calls, while the multiparametric statistical approach,  
175 which works with LMA parameters (Schrader and Hammerschmidt 1997) and parameters  
176 measured in Raven Pro 1.4 (Cornell Laboratory of Ornithology), were expected to perform  
177 similarly well on both tonal (harmonic) and atonal calls.

178

## 179 **Material and methods**

### 180 **Subjects**

181 Four captive grey parrots participated in this study: Durosimo (male), Jaro (male), Jarina  
182 (female), and Juruba (female). Durosimo, Jaro, and Juruba were part of a group that arrived  
183 from the Congo as subadults. Jarina was also wild born, with an unknown place of origin. At  
184 the time of recording, Durossimo, Jaro, and Juruba were 12 years old (based on seller's  
185 information). Jarina's age could not be determined. Durosimo, Jaro, and Juruba had never  
186 been handled by humans and were kept in an indoors aviary together. Jarina was habituated to  
187 human presence and handling. She had previously participated in language-learning  
188 experiments (see Giret et al. 2010). At the time of the recording, she had been kept together  
189 with the other three parrots for several years.

190 At the time of recording, subjects were kept together in one room. Each individual was  
191 housed in a cage measuring 90x60x60cm. The cages were placed about a meter apart, so the

192 parrots had visual and acoustic contact with each other. They could also hear other grey  
193 parrots in an adjacent room and various bird species living outside.

194

#### 195 Recordings

196 The parrots were recorded from June to November 2008 (on 23 and 27 June, 13 and 21 July, 4  
197 and 11 August, 31 October, and 1 November). Recording was conducted using Sennheiser  
198 ME 67 microphone and an external USB preamplifier MOBILEPRE-USB in 44 kHz (16 bits)  
199 wav format. The recording position was at the wall opposite the cages, app. 2m away from  
200 them, thus ensuring equal distance from all cages. This way, amplitude could be taken into  
201 account in subsequent analyses.

202 Most recording days consisted of three blocks: a morning block, a noon block, and an evening  
203 block. The morning block started shortly after dawn (e.g., 4:30 am in the summer) and the  
204 evening block ended at dusk (e.g., 9 pm in the summer). The noon block took place during the  
205 day, when the parrots were less vocally active (e.g. 9 am to 11 am in the summer). We  
206 included the noon block mainly into the early recording days to make sure we would not miss  
207 any categories that might be performed only in particular situations, such as feeding. It turned  
208 out, however, that parrots vocalize at this time of the day minimally and no new categories  
209 emerged. Later in the process, we have therefore omitted the noon block. Each recording  
210 block started with habituating the parrots to the recording situation and human presence. An  
211 observer entered the room with a microphone and sat quietly on a chair at the wall, facing the  
212 cages with parrots. Such habituation session preceded a recording session because our  
213 previous experience had indicated that parrots tend to change (or completely stop) their  
214 vocalizations after a human enters their room. In the initial sessions, the habituation lasted for  
215 half an hour, later it was adjusted to the parrots' reaction.

216 Each parrot was recorded for 15 minutes per block (3x15 minutes per day). In total, each  
217 individual was recorded 23 times and we obtained 345 minutes of recording. As shown in  
218 Figure 1, this recording time seems sufficient to describe the repertoire of the entire grey  
219 parrot group. Nevertheless, the repertoires of individual parrots could possibly expand until  
220 reaching the group numbers with additional recording time. During recording, the calls of a  
221 targeted individual were verbally marked on the recording by the observer. Marks directly  
222 followed the calls they related to and were not extracted with the calls. Individual calls were  
223 then manually demarcated using a spectrogram view and extracted from recordings into  
224 separate wav files using SoundForge 8.0. Calls that overlapped with background noise or with  
225 other parrots' calls were not included in the following analysis.

226 Analyses of recordings

227 *The visual-acoustic method (VA)*

228 Spectrograms were generated in SoundForge 8.0 with sample rate 22 kHz at 16 bits using a  
229 2048-point fast Fourier transform length, with Blackman-Harris smoothing window and 75%  
230 window overlap, frequency resolution 21.5 Hz, and time resolution 0.046s. In the visual-  
231 acoustic (VA) analysis, calls were sorted in categories that were based on acoustic perception  
232 and visual perception of the spectrograms. Categorization was executed qualitatively by  
233 several rounds of individual sorting of calls, followed by search for agreement and discussion  
234 of differences between categorizers. All categorizers were trained in behavioral observation  
235 and vocal analysis, had extensive personal knowledge of the birds, and had previously  
236 participated in parrot language training and other experiments with these subjects.

237 In the first step, three categorizers (A, B, and C) independently categorized calls they had  
238 previously recorded. They identified 22 (A), 67 (B), and 44 (C) categories. Their agreement  
239 was relatively low: categorizer B and C agreed on 35 categories, but only 2 of these matched

240 categories identified by categorizer A. In most cases, one category by categorizer A included  
241 calls sorted into two or more categories identified by categorizers B and C. Subsequently,  
242 only categorizers A and B worked on categorization. They discussed clusters of similar  
243 categories (or one of categorizer A's original categories) and sought ways in which finer  
244 categories – typically based on a previous categorization by categorizers B and C – could be  
245 distinguished within such clusters. Acoustic and visual spectrum characteristics used to  
246 distinguish the resulting categories included: tonality vs. noise, dominant frequency, spectrum  
247 bandwidth, intensity of harmonics, and frequency modulation (e.g. a rising or falling trend).  
248 When agreeing on a set of distinguishing characteristics, both categorizers independently  
249 sorted calls from a cluster into these proposed categories. If they reached at least 75%  
250 agreement of assigned calls, the category was accepted into final categorization. If not, a new  
251 category was proposed. A new category was adopted when at least three calls could be  
252 identified as belonging to it. Categories were tagged by letter “K” followed by a number  
253 representing the frequency of calls belonging to the category in question (so that, e.g., K1 was  
254 the most frequently used category). The final set of categories was further split in clusters of  
255 similar categories of calls based on categorizers' A and B consensus. These clusters were then  
256 used in the multiparametric statistical method (see below).

257

### 258 *Spectrographic cross-correlation (SPCC)*

259 From calls categorized by the visual-acoustic method, we extracted a sample for the  
260 spectrographic cross-correlation (SPCC) method. The sample consisted of ten randomly  
261 selected calls for each of the four parrots in each of the 70 categories defined during the  
262 process described above. If a parrot produced ten or less calls in a category, all were included.  
263 The final sample consisted of 1,516 calls. We performed batch correlations in Raven Pro 1.4  
264 by comparing spectrograms of all calls from the individual categories.

265 Spectrograms were calculated with 512 samples, 3dBFilter Bandwidth 135 Hz, hop size 256  
266 samples, and grid spacing 93.8 Hz, using a 512-point discrete Fourier transform length with a  
267 Hann smoothing window and 50% window overlap, frequency resolution 86.1 Hz, and time  
268 resolution 0.012s. For each category, we computed a “category correlation matrix”, that is, a  
269 correlation matrix of peak correlations within a category. Similarity of calls within a category  
270 (which we further refer to as “inner consistency”) was calculated as the average of all values  
271 in the category correlation matrix. We set the lower boundary of inner consistency – used as  
272 an indicator of sufficient similarity of calls within a category – to 0.2 because individual calls  
273 in 11 categories sounded very similar to human ear but had inner consistency only between  
274 0.2 and 0.3. Subsequently, we employed the VA method to select for each category several  
275 other categories (“outgroups”) with similar acoustic and visual parameters and/or a likely  
276 overlap of calls categorized into the assessed and the outgroup category. For each assessed  
277 category–outgroup pair, we calculated an “outgroup correlation matrix”, i.e., a correlation  
278 matrix of peak correlations between calls from the assessed category and calls from its  
279 outgroup category. T-tests comparing correlation coefficients in the category correlation  
280 matrix with outgroup correlation matrix were used to test whether similarity of calls within a  
281 category is greater than the similarity of calls between this category and another category  
282 (outgroup). If inner consistency was not significantly higher than the outgroup correlation, we  
283 considered merging the assessed category with its outgroup.

284

### 285 *The multiparametric statistical (MS) method*

286 For the multiparametric statistical (MS) method, we used the same sample of calls as for the  
287 SPCC method. From the spectrograms, we measured a number of acoustical parameters using  
288 automatic algorithms. Spectrograms were processed using the same parameters as in the  
289 SPCC method in Raven Pro 1.4 (Cornell Lab of Ornithology). Eight parameters were

290 measured using semi-automatic measurements (manual demarcation of a call and an  
291 automatic computation) in Raven Pro 1.4. Demarcation of calls was based on visual  
292 detectability of the sound in a spectrogram. In Raven Pro 1.4, the parameters were: *High*  
293 *Frequency [Hz]* (the upper frequency boundary of call selection), *Center Frequency [Hz]*(the  
294 frequency which divides the call selection in two frequency intervals of equal energy), *Energy*  
295 *[dB]* (the total energy of call selection), *Interquartile Range Bandwidth [Hz]* (difference  
296 between the first and third quartile frequencies, where quartiles describe the distribution of  
297 energy of a call on the frequency axis), *Interquartile Range Duration [s]* (difference between  
298 the first and third quartile times, where quartiles describe the distribution of energy of a call  
299 on the time axis), *Length* (the number of frames contained in a call selection), *Max Power*  
300 *Frequency [Hz]* (the frequency at which Max Power occurs within the call selection), *Max*  
301 *Power[dB re 1]* (maximum power in the call selection) (Charif et al. 2010). Additionally, the  
302 spectrograms were analyzed with LMA 2008 software (Schrader and Hammerschmidt 1997).  
303 A set of 12 temporal and frequency parameters was used, many of which measure the  
304 statistical distribution of frequency amplitudes in the spectrum (DFA) or describe the first  
305 three dominant frequency bands (DFB). DFA values mark the frequency at which amplitude  
306 distribution in the spectrum reaches the first, second, and third quartile of total distribution.  
307 DFB are defined by amplitudes that exceed a given threshold in a consecutive number of  
308 frequency bins. We employed the following measurements: *q1mean [Hz]* (mean frequency of  
309 the first DFA), *q2mean [Hz]*, (mean frequency of the second DFA), *q3mean [Hz]* (mean  
310 frequency of the third DFA), *df1mean [Hz]* (mean frequency of the first DFB), *df1chfre*  
311 (number of changes between the original and floating average curve of the first DFB),  
312 *df1maloc* (location of the maximum frequency of first DFB), *df2mean [Hz]* (mean frequency  
313 of the second DFB), *df3 mean [Hz]* (mean frequency of the third DFB), *ranmean [Hz]* (mean  
314 frequency range), *pfmax [Hz]* (the highest of frequencies with peak power established in

315 consecutive time segments during a call), *pfmean* [Hz] (mean peak frequency), and *pfjump*  
316 [Hz] (the maximum difference of peak frequency in two consecutive time segments). Both  
317 LMA and Raven parameters were used because LMA parameters had been defined mainly for  
318 atonal calls (Schrader and Hammerschmidt 1997). They could thus be less well suited for  
319 tonal and harmonic calls, which is what Raven parameters should compensate for.  
320 Subsequently, we applied a forward stepwise discriminant function analysis (DF) to confirm  
321 the VA categorization. To validate the results of discriminant analysis, we implemented a  
322 cross-validation process based on leave-one-out method in IBM SPSS Statistics for Windows,  
323 Version 21.0. Since the DF can discriminate between a limited number of categories, it was  
324 applied to clusters of similar call categories established by the VA method (see Table 3).  
325 Clusters were tagged by letter “C” followed by a number representing the frequency of use of  
326 that cluster (so that C1 was the most frequently used cluster).

327 We compared the results of these methods. The SPCC method and the MS approach resulted  
328 in recommendations to merge several call categories. We compared the merging suggestions  
329 from the two methods and where both computer-aided methods proposed the same merger,  
330 the categories were merged. If the merger was proposed only by one computer-aided method,  
331 it was revised by a repeated inspection of VA features of the categories concerned.

332

### 333 **Results**

334 We obtained a total of 3,052 calls from our four subjects. Three subjects were similarly  
335 vocally active (Jaro 29.23% of all recorded calls, Juruba 28.15%, Jarina 26.34%), while  
336 Durosimo produced less vocalizations (16.32%).

337 Using the VA categorization, we identified 70 categories containing 3 to 238 calls (see Table  
338 1). No individual used all categories (see Table 2a) but the 20 most frequent categories were  
339 detected in all parrots. Categories were classified into 18 clusters (see Table 3).

340 The SPCC method resulted in a reduction of categories to 47. Thirty-three VA-determined  
341 categories had a sufficiently high inner consistency (above 0.2) and correlations in the  
342 category matrix were significantly lower than correlations in all tested outgroup correlation  
343 matrices as measured by a t-test. The remaining 14 categories were formed by merging two  
344 (nine cases), three (three cases), or four (two cases) categories determined by the VA analysis.  
345 We decided to merge these categories because their outgroup correlations did not differ from  
346 their inner consistencies (when compared by t-tests) and/or they showed a low inner  
347 consistency (under 0.2). For t-tests results, see Table S1. Two categories with low inner  
348 consistency were discarded since no attempted merging with an outgroup led to inner  
349 consistency of such new category above 0.2 (see Table 1).

350 Similarly, the MS approach resulted in a reduction of the number of categories formed by the  
351 VA method. In 10 (out of 18) clusters, a merger of two or more categories led to more precise  
352 discrimination between categories (see Table 3). We considered a merger when over 25% of  
353 calls were classified into a different category. From the 70 categories established by the VA  
354 method, 46 were well established in the MS approach. Nine “new” categories were suggested  
355 by merging two (six cases), three (two cases), or four (one case) categories. Two categories  
356 were excessively scattered and discarded due to no suitable merging category. The total  
357 number of categories proposed after implementation of the MS approach was 55 (see Table 1).

358 In seven cases, there was an agreement between the SPCC and MS approach on which VA-  
359 established categories should be merged. In another seven cases, however, the merger was  
360 proposed only by one of the methods, which led to a re-inspection of the VA features of the



361 categories in question. Overall, 51 (72.9%) categories determined by the VA could be  
362 confirmed by at least one of the two computer-aided methods.

363

## 364 **Discussion**

365 The use of computer-aided methods resulted in a relatively extensive confirmation of  
366 categories established by the VA method. In particular, computer-aided methods helped verify  
367 the discrimination of VA categories and confirm similarity among calls falling into the same  
368 VA category (relative to calls classified into other VA categories).

369 The VA method allowed for the formation of a relatively high number of categories  
370 characterized by high acoustic and visual coherence but the differentiation threshold among  
371 categories was sensitive to the subjectively variable perception of each categorizer. The SPCC  
372 method was based on an objective mathematical comparison of calls but even here, a  
373 subjective element was present: for instance, thresholds had to be set by categorizers to define  
374 sufficient consistency of a category. The shortcomings of SPCC method had to do with  
375 distinctiveness: lack of distinction between some similar categories may have been due to  
376 SPCC's low sensitivity with respect to atonal and noisy calls that lacked clear frequency  
377 contours. The MS method was capable of distinguishing among relatively acoustically close  
378 categories of both noisy and harmonic calls thanks to its reliance on a combination of  
379 parameters suited to both atonal and tonal/harmonic calls. Nevertheless, while the DF has  
380 been efficiently used in studies with a lower number of categories (e.g. Hedwig et al. 2014,  
381 Price et al. 2014), differentiation among a higher number of categories using this method is  
382 problematic (Zdenek et al. 2015). We have therefore set the upper limit to ten categories and  
383 performed a discriminant analysis on clusters of similar categories. Generally speaking, unlike  
384 the VA method, computer-aided methods do not evaluate a sound as a whole. They usually

385 extract only part of information contained in a sound and that may be insufficient. Divergence  
386 between computer-aided methods may be due to differences in parameters they take into  
387 account when analyzing calls. Human categorizers are capable of assessing sounds  
388 holistically. An ideal computerized method would, similarly, find all parameters that capture  
389 the acoustic variability detected by the VA method. At present, neural network approaches  
390 seem to be closest to this goal but they need extensive training with preprocessed data and the  
391 resulting extracted categorization rules are hard to interpret.

392 Although we do not know to what extent grey parrots' intraspecific acoustic perception  
393 system tends to sort calls into discrete categories or rather process them within a continuous  
394 gradient or to what level of detail parrots themselves distinguish their calls, based on  
395 following indirect indices we suggest that the perception categories identified by the VA  
396 method are close to what parrots themselves may perceive as distinct. Despite lack of studies  
397 on grey parrots' acoustic perception, it is reasonable to assume that to process sounds as  
398 discrete categories of calls is these birds' natural ability and their acoustic perception operates  
399 in similar ranges as in humans. Given that perception is needed for reproduction, this  
400 assumption of similarity finds support in parrots' ability to accurately reproduce human  
401 vocalizations, to discriminate between phones and to reuse learned strings of phones in  
402 producing new words (Bottoni et al. 2009; Patterson and Pepperberg 1998; Pepperberg 2010).  
403 Auditory studies on budgerigars (Okanoya and Dooling 1987) and orange-fronted conures  
404 (Wright et al. 2003) suggest that there are both possible parallels and differences between  
405 humans, parrots, and songbirds. For most songbirds and parrots tested, the regions of best  
406 auditory sensitivity corresponded to the optimal range of human auditory sensitivity (2–5  
407 kHz) (Dooling 1980; Wright et al. 2003). On the other hand, birds in general are better at  
408 discriminating absolute pitch (Weisman et al. 2004). Playback experiments in grey parrots

409 would be required to evaluate their sound perception abilities and their similarities with and  
410 differences from human ones.

411 Our results suggest that a combination of the VA method with one or more computer-aided  
412 methods could be well suited to analysis of the vocal repertoire of grey parrots. This  
413 corresponds to the findings of Giret et al. (2011). Nevertheless, the computer-aided methods  
414 used in this study all turned out to have some weaknesses and each performed well only on  
415 part of the parrots' rich and complex vocal repertoire.

416

## 417 **Study 2: Intergroup repertoire comparison**

418 In Study 2, we used the repertoire established by the VA method to preserve the methodology  
419 employed in Giret et al. (2012), which we used as a comparative material. In particular, we  
420 used the typical calls of each category to compare the repertoire of two individuals. Typical  
421 calls (prototypes) for our parrot's repertoire were determined by the SPCC as calls with the  
422 highest average of peak correlations with every call in a given category. Prototypes for the  
423 other parrot's repertoire were identified in a similar manner. One could expect that by using  
424 typical calls, we would maximize the distinctiveness of calls from different categories and  
425 lower the likelihood of finding a similarity between two compared repertoires.

### 426 **Subjects**

427 We performed a comparison of repertoires of two female grey parrots, Zoé and Juruba. The  
428 grey parrot Zoé from a French laboratory had been hand-reared in captivity and purchased  
429 from breeders. She arrived at the French laboratory in September 2003 aged 3 months. Since  
430 her arrival at the laboratory, she has been in close contact with humans and was trained to  
431 referentially imitate French labels. She was housed with three other grey parrots in an indoor  
432 aviary. From the aviary, Zoé could hear domestic canaries and various noises.

433 For the comparison, we chose Juruba, a female grey parrot from the Czech laboratory who  
434 produced the largest number of categories of sounds. Zoé and Juruba had never seen nor  
435 heard each other and had no previous contact with any member of the other parrot's social  
436 group. See Study 1 for information on Juruba from the Czech laboratory.

437

## 438 **Material and methods**

439 Zoé had been recorded regularly since her arrival at the laboratory in September 2003 until  
440 March 2007, i.e., from the age of three months until four years of age. All recordings were  
441 conducted in 22 kHz (16 bits) wav format with high-quality microphones. For further details,  
442 see Giret et al. (2012). For details on recording Juruba, see above in Study 1. The sampling  
443 rate of the two sets of recordings was the same and spectrograms were created using identical  
444 parameter settings. Both laboratories collected their recordings indoors, leading to both sets of  
445 calls being similarly affected by resonance and relatively low noise. There was a significant  
446 difference between the two individuals' recording periods: the relatively short recording  
447 period in Juruba may have somewhat reduced the number of call categories identified for her  
448 (see Figure 1).

449 We selected one prototype for each call category in the repertoire of each parrot. The set of  
450 prototypes for Juruba included 62 calls (Figure 2). The set of prototypes for Zoé contained  
451 100 calls (Figure 3), whereby none were imitations of the French labels. Comparison  
452 between the two sets of prototypes was performed by the VA method in a two-step procedure.  
453 In the first step, the repertoires were compared by two independent categorizers (B and D)  
454 who tried to match Juruba's and Zoé's prototype calls. The categorizers mostly chose at most  
455 two possible call counterparts but in six cases, one categorizer chose three or four possibilities.  
456 Agreement between these two main categorizers on either assigning the same counterpart to a

457 call or finding no counterpart was 51.6%. In the second step, we therefore recruited two  
458 additional trained categorizers (E and F), who re-evaluated the cases of disagreement between  
459 categorizers B and D and decided between the counterparts suggested by them. In 100% cases,  
460 expert discussion concerning the problematic calls led to an agreement between the two new  
461 categorizers and one of the primary categorizers.

## 462 **Results**

463 Thirty-two (51.6%) calls from Juruba's set of prototypes were matched to similar calls in  
464 Zoé's set of prototypes (Figure 4). Similarly, 29 (29%) of Zoé's prototype calls were matched  
465 to similar calls in Juruba's set. In five cases, Zoé's calls matched two counterparts from  
466 Juruba's repertoire. In contrast, the two females from the Czech laboratory, Juruba and Jarina,  
467 share on average 88.4% ( $SD = 7.8$ ) of their repertoire and average similarity of repertoires  
468 between any two parrots from the Czech laboratory is 84.4% ( $SD = 6.2$ ) (see Table 2b). From  
469 the 70 categories determined by the VA method, all four parrots from the Czech group  
470 performed 37 categories (52.9%) at least once, while three of the four parrots shared  
471 additional 19 categories (27.1%), 12 categories (17.1%) were shared by two individuals, and  
472 the two remaining categories (2.9%) were produced only by Jaro, the male. Juruba herself, in  
473 addition to sharing 37 categories (59.7%) with all three other parrots from her social group,  
474 shared 17 additional categories (27.9%) with two parrots, and eight categories (13.1%) with  
475 one parrot. Nineteen (59.4%) of the categories shared between Juruba and Zoé were also  
476 shared by all four individuals in Juruba's social group. Another eight categories (25.8%) of  
477 those which Juruba shared with Zoé were also shared between Juruba and two individuals  
478 from her group, while the remaining five categories (16.1%) were shared between Juruba and  
479 one individual from her group.

480

## 481 **Discussion**

482 We found a relatively large proportion of shared calls in the repertoires of two grey parrots  
483 who never had any vocal contact with each other nor any member of the other parrot's social  
484 group and who were surrounded by humans speaking different languages (Czech in Juruba's  
485 case, French in Zoé's). Over half and over a fourth of calls produced by parrots with the  
486 smaller and larger repertoire, respectively, were shared between the two. Giret et al. (2012)  
487 lists only three categories allegedly used by all grey parrots. The first shared call, described as  
488 "squawk", was identified by Cruickshank et al. (1993), Giret et al. (2012), and May (2004). It  
489 is similar to our K8 category. The call was detected either during excitement (Giret et al.  
490 2012) or in preflight and agonistic situations (May 2004). The other two shared calls  
491 suggested by Giret et al. (2012) were emitted during distress and in agonistic interactions.  
492 Those calls were not found in Juruba's repertoire, but they do appear in the repertoire of other  
493 individuals kept in our laboratory (data not shown).

494 A comparison between the proportion of calls that Juruba shared with members of her group  
495 and with the unfamiliar conspecific, Zoé, gives us some idea about the role of social learning  
496 in the establishment of vocal repertoire in grey parrots. Nevertheless, interpretation of calls  
497 shared within a group as socially learned as well as assumption that (only) calls shared  
498 between two distant individuals are possibly based on some innate predispositions are to some  
499 extent tentative.

500 We observed a high proportion of calls shared within a group. It is likely that this proportion  
501 may have been even higher had the recording period been expanded, eventually approaching  
502 100% of the group repertoire, as indicated by Figure 1. Nevertheless, individual call  
503 categories can be either socially learned, learned from environment, or "invented" (e.g. by  
504 vocal play) by an individual parrot. Interestingly, for Juruba, Jarina, and Durosimo, we  
505 observed no calls specific to individuals. Only the male, Jaro, produced two call types never

506 recorded in another group member. Still, it is possible that group members learned calls  
507 originally performed by Juruba or they may have developed the same calls independently,  
508 perhaps due to a shared innate predisposition (and for some reason, such as some  
509 characteristics of the acoustic environment, such calls were not recorded in Zoé although she  
510 inherited the same predisposition). One thus cannot conclusively claim that all calls shared by  
511 members of our group and not shared with Zoé were socially learned by Juruba. Secondly,  
512 call sharing could be the result of parrots' parallel learning from members of other species or  
513 from their inanimate environment.

514 At the same time, the relatively large proportion of calls shared by two isolated individuals  
515 indicates that there may be common call categories that have a high probability to appear in  
516 all grey parrot populations by all grey parrot populations. Nonetheless, it is most likely that  
517 the results we obtained are but an inaccurate estimate of similarity of vocalizations in distinct  
518 grey parrot populations. First of all, this is due to the subjective nature of our methods of  
519 repertoire establishment and comparison. Moreover, our recording plot (Figure 1) indicates  
520 that had we continued recording, Juruba's repertoire may have expanded until reaching the  
521 levels observed for the whole group numbers, which could lead to additional identifications of  
522 calls shared by the two females, Juruba and Zoé. In short, the larger proportion of unmatched  
523 calls in Zoé's repertoire in comparison to Juruba's repertoire could be simply due to the fact  
524 that Zoé had been recorded over several years or due to different thresholds for categories in  
525 each laboratory, which may have resulted in a more detailed categorization of Zoé's vocal  
526 sample. Moreover, our comparison focused on sorting calls into certain categories and did not  
527 deal with the fact that calls assigned to one category can still be similar to varying degrees,  
528 whereby parrots themselves might infer important information from the perception of a  
529 continual degree of similarity apart from identification of a call type.

## 530 **General discussion**

531 A comparison of vocal repertoires of two parrot individuals from different and separate  
532 settings indicates the existence of a substantial overlap in the repertoires of distinct grey  
533 parrot populations. No previous study identified such a large proportion of intergroup shared  
534 calls within this parrot species that is assumed to have the capacity of open-ended vocal  
535 learning (Giret et al. 2012). Nevertheless, Salinas-Melgoza and Wright (2012) presented some  
536 evidence of possible limitations to vocal learning in adult yellow-naped amazons and it is  
537 likely that some calls tend to reappear in vocally isolated groups based on inherited  
538 predispositions, in a manner similar to that which has been reliably documented for songbirds  
539 (Gardner et al. 2005, Fehér et al. 2009).

540 Similar vocal patterns in independent grey parrot populations with shared innate vocal  
541 predispositions may have simply developed by vocal play, that is, without any specific  
542 external acoustic input. Learning of species-typical songs by “invention”, i.e., learning not  
543 obviously related to tutor song, has been described in songbirds (Beecher & Brenowitz, 2005).  
544 In the case of parrots, acquisition of new calls by a related mechanism called “vocal play” has  
545 been proposed (Pepperberg 1999). In human language development, vocal play allows  
546 children to explore the potential of their vocal tract by making new phonemic combinations  
547 from preexisting labels (Stark 1980). A form of vocal play called “monologue speech,” which  
548 refers to active communication without social stimulation, that is, vocalization in solitude  
549 (Kuczaj 1983), has been detected in the grey parrot Alex and it is assumed it accelerated his  
550 learning (Pepperberg 1999, 2002). While this mechanism obviously bears similarity to the  
551 “subsong” known in songbirds (Marler 1970), it may also work analogically as in humans  
552 when we consider learning of a physiologically limited variety of syllables (Ohala 1983).

553 At the same time, there is no doubt that social learning does influence the vocal repertoire of  
554 grey parrots. Our results confirm it: birds from the same group shared substantially more calls  
555 than one of them, Juruba, shared with the unfamiliar conspecific, Zoé. It is yet unknown



556 whether in grey parrots, vocal learning in a social group focuses on mimicking new call types  
557 or modification of already familiar calls by, e.g., changing their pitch, modulation, addition of  
558 new elements, etc. A study on the dialects of amazon parrot seems to indicate that gradual  
559 modification of pre-existing calls is a likely option (Salinas-Melgoza & Wright 2012). Pair  
560 call convergence in budgerigars indicates that both options are possible, because males seem  
561 to imitate new calls from female repertoire, whereas females only slightly change their own  
562 contact call (Hille et al. 2000). If the latter mechanism is prevalent, we could expect to find  
563 the same call categories in different groups, although calls within a category would resemble  
564 each other more closely among members of one social group than between unfamiliar  
565 individuals. Future research into the level of similarity between calls of the same category  
566 could shed more light on this topic.

567 Generally speaking, the adaptive function of extensive vocal learning in parrots remains  
568 unclear. Nowicki and Searcy (2014) offer five possible explanations for the origin of vocal  
569 production learning in animals: 1) the vocal dialect hypothesis, which states that vocal  
570 learning supports geographic variation in vocal signals and that facilitates local assortative  
571 mating and promotes local adaptation, 2) the sexual selection hypothesis, which explains  
572 repertoire expansion as a response to mating preference for more complex vocalizations, 3)  
573 the information sharing hypothesis, which explains vocal learning by the need to share  
574 information among kin, 4) the environmental adaptation hypothesis, which emphasizes vocal  
575 adaptation to local habitat, and 5) the individual recognition hypothesis, which claims that  
576 vocal learning allows for the emergence of individually specific vocal signals. The vocal  
577 dialect hypothesis (1) and sexual selection hypothesis (2) are not a likely explanation in grey  
578 parrots because there is no evidence that specific mating calls and preferences for local mates  
579 belong among behavioral strategies found in this species. The information sharing hypothesis  
580 (3) is also unlikely to be the case, because information sharing among kin by complex vocal

581 communication has not been demonstrated in any nonhuman species. Both the environmental  
582 adaptation hypothesis (4) and individual recognition hypothesis (5) seem to be at least partly  
583 applicable to grey parrots. These hypotheses find support in grey parrots' extraordinary  
584 mimicking abilities both in the wild and in captivity (Cruickshank et al. 1993; Giret et al.  
585 2012; May 2004; Pepperberg 1999) and their ability to recognize each other as individuals by  
586 vocal communication (Giret et al. 2009; May 2004). Bradbury and Balsby (2016), however,  
587 suggest that the most likely explanation for the evolution of vocal learning in parrots is their  
588 need for warbles or duets used in nest defense and in the acquisition and modulation of  
589 contact calls which mediate social dynamics. So far, the most direct support for this proposal  
590 comes from studies which show that male budgerigars in captivity mimic the calls of females  
591 during courtship (Hile et al. 2000). In future studies, it would be interesting to look at calls  
592 shared in grey parrot bonded pairs.

593 We suppose that our group of grey parrots may use vocal learning to converge their vocal  
594 repertoires and thus strengthen the bonds within their social group, because call convergence  
595 in groups has been demonstrated in various songbird and parrot species (Balsby and Bradbury  
596 2009; Berg et al. 2012; Enggist-Dueblin and Pfister 2002; Hile and Striedter 2000; Sewall  
597 2009). The bonding effect of vocal learning in a group can be partly responsible for the  
598 outstanding "linguistic" abilities of Alex, who was very close to his caregiver (Pepperberg  
599 1999) and for the disappointing results of the Model/Rival method in the study by Giret et al.  
600 (2010), where the parrots bonded with their caregivers to a much smaller extent. It has also  
601 been shown that grey parrots have little interest in learning vocalizations from playback (Giret  
602 et al. 2010; Pepperberg and Mclaughlin 1996). It seems they prefer vocal learning in  
603 interaction with a live partner who is part of their social group.

604 The system of vocal learning resting on a shared vocal base could be evolutionary adaptive  
605 here. When conspecifics with different life histories meet, a shared vocal base might help

606 them learn from each other. Such system could facilitate flexible convergence of repertoires  
607 in mating pairs and assimilation of new members into established groups. For future research,  
608 it would be interesting to verify the bonding function of social learning of vocal repertoire, for  
609 instance by experimentally manipulating individuals' membership in a group.

610 To map the repertoire of grey parrots, we used a combination of three methods. Outcomes of  
611 the VA method were for the most part confirmed by the SPCC or the MS method or both.  
612 SPCC was capable of distinguishing finer differences among harmonic calls, while the MS  
613 performed well on both harmonic and atonal calls because it relied on a combination of  
614 parameters suited to both atonal and tonal/harmonic calls. The comparison method used in  
615 Study 2 was similar to the VA method used in Study 1 but adapted to a different task. Both  
616 methods started with independent classifications of calls by two or three trained categorizers.  
617 This generated a relatively low agreement but one ought to keep in mind that the level of  
618 chance agreement was extremely low. Initial classification was therefore followed by  
619 discussions regarding disagreements among categorizers until a consensus was reached. In  
620 Study 1, discussions focused on establishing characteristics that define a category. This led to  
621 agreement on a finer classification of calls. In Study 2, two additional trained categorizers  
622 were called in to find consensus with one of the primary categorizers. A combination of the  
623 more subjective VA method conducted by human observers and computer-aided methods led  
624 to increased reliability of the final categorization of grey parrot vocal repertoire. Various  
625 clustering methods, especially fuzzy c-means clustering (Wadewitz et al. 2015), might bring  
626 some additional advances to mapping of vocal repertoire and deal with the possibility that  
627 grey parrot's acoustic perception could, to some extent, have the form of continuous acoustic  
628 gradient processing.

629 In this study, we worked with a small group of individuals. Small numbers of subjects are  
630 common in laboratory studies of parrot behavior and communication due to inherent technical

631 limitations. Due to small sample size, the findings presented here cannot be directly  
632 generalized to the species as a whole. They can, however, be viewed as a starting point for  
633 future replication studies on different individuals from distinct social groups.

634 This study demonstrated the extent of similarity among repertoires of individual grey parrots  
635 from different social groups. The logical next step towards a greater understanding of the  
636 structure and dynamics of great parrots' vocal communication would take the form of  
637 observation of how group repertoire evolves over time and how it may be affected by changes  
638 in a social group. In particular, it would be interesting to observe whether long-term  
639 cohabitation or bonding of grey parrots leads to an increase in the shared repertoire or not, i.e.,  
640 whether individual variability of calls in a group or dyad remains unchanged. It would also be  
641 interesting to find out whether vocal conversion is based on the mimicking of new calls or  
642 modification of pre-acquired ones, and what role grey parrots' disposition to produce a certain  
643 set of call categories plays in these processes.

644

645 **Ethical approval:** "All applicable international, national, and/or institutional guidelines for  
646 the care and use of animals were followed."

647

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821

822 **Table 1:** Call categories identified with the visual-acoustic (VA) method and confirmed by  
 823 computer-aided spectrographic cross-correlation (SPCC) and multiparametric statistical (MS)  
 824 method in a captive group of grey parrots

VA Category	Count	SPCC	MS	Inner consit. (SPCC)	Higher outgroup correlations (SPCC)	Final Category
K1	238	✓	✓	0.392		K1
K2	191	✓	✓	0.200		K2
K3	179	✓	m <sup>K32</sup>	0.210		K3
K4	156	m <sup>K38,K63</sup>	m <sup>K38</sup>	0.616		K4 + K38
K5	130	m <sup>K28,K30,K58</sup>	m <sup>K30,K35,K39</sup>	0.518	0.543 <sup>K30</sup>	K5 + K30
K6	107	m <sup>K11</sup>	✓	0.224		K6
K7	92	✓	✓	0.369		K7
K8	92	m <sup>K40</sup>	m <sup>K40</sup>	0.517		K8 + K40
K9	89	✓	✓	0.290		K9
K10	85	✓	✓	0.255		K10
K11	80	m <sup>K6</sup>	✓	<u>0.167</u>	0.182 <sup>K6</sup>	K11
K12	78	m <sup>K45</sup>	✓	0.374		K12
K13	76	✓	m <sup>K22,K29</sup>	0.292		K13
K14	70	✓	✓	0.223		K14
K15	57	✓	✓	0.659		K15
K16	54	✓	✓	0.490		K16
K17	53	✓	✓	0.337		K17
K18	51	✓	✓	0.433		K18
K19	50	m <sup>K21,K24</sup>	m <sup>K21,K24</sup>	0.437		K19 + K21 + K24
K20	50	✗	✗	<u>0.151</u>	0.170 <sup>K63*</sup>	✗
K21	48	m <sup>K19,K24</sup>	m <sup>K19,K24</sup>	0.221	0.234 <sup>K14</sup> 0.316 <sup>K19</sup>	K19 + K21 + K24
K22	45	m <sup>K29</sup>	m <sup>K13,K29</sup>	0.360		K22 + K29
K23	44	m <sup>K67</sup>	✓	0.635		K23
K24	43	m <sup>K19,K21</sup>	m <sup>K19,K21</sup>	0.338	0.390 <sup>K19</sup>	K19 + K21 + K24
K25	41	✓	✓	0.302		K25
K26	40	m <sup>K56,K68,K69</sup>	m <sup>K68</sup>	<u>0.165</u>	0.180 <sup>K56</sup> 0.190 <sup>K68</sup> 0.285 <sup>K69</sup>	K26 + K68
K27	38	m <sup>K64</sup>	m <sup>K66</sup>	0.488		K27
K28	38	m <sup>K5,K30,K58</sup>	✓	0.442	0.474 <sup>K23</sup> 0.561 <sup>K30</sup> 0.452 <sup>K67</sup>	K28
K29	38	m <sup>K22</sup>	m <sup>K13,K22</sup>	0.268	0.269 <sup>K22</sup>	K22 + K29
K30	35	m <sup>K5,K28,K58</sup>	m <sup>K5,K35,K39</sup>	0.465	0.543 <sup>K5</sup> 0.494 <sup>K23</sup> 0.494 <sup>K28</sup>	K5 + K30
K31	33	✓	✓	0.360		K31
K32	28	✓	m <sup>K3</sup>	0.367		K32
K33	28	✓	✓	0.317		K33
K34	28	m <sup>K52</sup>	✓	0.421		K34
K35	28	m <sup>K39</sup>	m <sup>K5,K30,K39</sup>	0.473		K35 + K39
K36	27	✓	✓	0.325		K36
K37	26	✓	✓	0.206		K37
K38	25	m <sup>K4,K63</sup>	m <sup>K4</sup>	0.421	0.498 <sup>K4</sup>	K4 + K38
K39	25	m <sup>K35</sup>	m <sup>K5,K30,K35</sup>	0.405	0.456 <sup>K5</sup> 0.440 <sup>K23</sup> 0.422 <sup>K28</sup> 0.414 <sup>K30</sup> 0.531 <sup>K35</sup>	K35 + K39
K40	24	m <sup>K8</sup>	m <sup>K8</sup>	0.369	0.420 <sup>K8</sup>	K8 + K40
K41	23	✓	✓	0.301		K41
K42	22	✓	✓	0.297		K42
K43	21	✓	✓	0.298		K43
K44	21	✓	✓	0.451		K44
K45	21	m <sup>K12</sup>	✓	<u>0.175</u>	0.212 <sup>K12</sup>	K45
K46	21	m <sup>K51</sup>	✓	0.488		K46
K47	20	✗	✗	<u>0.125</u>		✗
K48	19	✓	✓	0.281		K48
K49	18	✓	✓	0.630		K49
K50	17	✓	✓	0.546		K50
K51	17	m <sup>K46</sup>	✓	0.335	0.383 <sup>K46</sup>	K51
K52	15	m <sup>K34</sup>	✓	<u>0.156</u>	0.258 <sup>K34</sup> 0.243 <sup>K36</sup>	K52
K53	13	m <sup>K57,K70</sup>	✓	0.620	0.622 <sup>K70</sup>	K53
K54	13	✓	✓	0.419		K54
K55	12	✓	✓	0.409		K55
K56	12	m <sup>K26,K68,K69</sup>	✓	0.221	0.244 <sup>K69</sup>	K56
K57	11	m <sup>K53,K70</sup>	m <sup>K70</sup>	0.633	0.676 <sup>K49</sup>	K57 + K70
K58	11	m <sup>K5,K28,K30</sup>	✓	0.466	0.490 <sup>K5</sup>	K58
K59	11	✓	✓	0.481		K59
K60	9	✓	✓	0.453		K60
K61	9	✓	✓	0.507		K61
K62	9	✓	✓	0.313		K62
K63	8	m <sup>K4,K38</sup>	✓	0.363	0.438 <sup>K38</sup> 0.397 <sup>K4</sup>	K63
K64	8	m <sup>K27</sup>	✓	0.383	0.403 <sup>K27</sup>	K64
K65	7	✓	✓	0.469		K65
K66	6	✓	m <sup>K27</sup>	0.449		K66
K67	6	m <sup>K23</sup>	✓	0.305	0.397 <sup>K5</sup> 0.476 <sup>K23</sup> 0.414 <sup>K28</sup> 0.428 <sup>K30</sup> 0.348 <sup>K35</sup> 0.338 <sup>K39</sup>	K67
K68	5	m <sup>K26,K56,K69</sup>	m <sup>K26</sup>	0.220	0.404 <sup>K69</sup>	K26 + K68
K69	4	m <sup>K26,K56,K68</sup>	✓	0.578		K69
K70	3	m <sup>K53,K57</sup>	m <sup>K57</sup>	0.695		K57 + K70

825

- 826 Note:
- 827 ✓ ... category confirmed by the respective computer-aided method;
- 828 m ... category merged (with category or categories shown in the upper index);
- 829 ✗ ... category discarded;
- 830 VA category... name of a category determined by the VA method;
- 831 Count... the number of times the category was used by all parrots;
- 832 SPCC... confirmation, merging, or discarding indicated by the SPCC method;
- 833 MS... confirmation, merging or discarding indicated by the MS method;
- 834 Inner consistency (SPCC method) ... calculated as the average of values from the peak correlation matrix for a category, estimates the
- 835 similarity of calls within a category;
- 836 Higher outgroup correlations (SPCC method) ... cases when outgroup correlation was higher than inner consistency;
- 837 Final category ... categories proposed after performing both computer-aided methods.
- 838

839 **Table 2a:** The use of call categories by individual parrots

<b>Parrot</b>	<b>Number</b>	<b>%</b>
<b>Durosimo</b>	57	81.43%
<b>Jarina</b>	52	74.29%
<b>Jaro</b>	60	85.71%
<b>Juruba</b>	62	88.57%

- 840 Note: The number of categories used by a parrot (out of the 70 categories determined by the VA method).
- 841
- 842
- 843

844 **Table 2b:** Comparison of use of categories by individual parrots

	<b>Durosimo</b>	<b>Jarina</b>	<b>Jaro</b>	<b>Juruba</b>
<b>Durosimo</b>		77.19%	91.23%	87.72%
<b>Jarina</b>	84.62%		82.69%	94.23%
<b>Jaro</b>	86.67%	71.67%		85.00%
<b>Juruba</b>	81.97%	80.33%	83.61%	

845 Note: Percentage of shared categories between individual parrots determined by the VA method.

846

847 **Table 3:** Confirmative classification of calls into categories by the multiparametric statistical  
848 method.

<b>Cluster</b>	<b>Category</b>	<b>Correct classification</b>	<b>Validated</b>	<b>Merged/ Discarded</b>	<b>Classification after merging</b>	<b>Validated after merging</b>
C1	K1, K2, K15	91%	88%	-	-	-
C2	K7, K9, K13, K22, K29, K42, K55, K60, K61	76%	70%	m <sup>K13, K22, K29</sup>	85%	80%
C3	K5, K23, K28, K30, K35, K39, K67	57%	53%	m <sup>K5, K30, K35, K39</sup>	79%	76%
C4	K14, K18, K19, K21, K24	63%	56%	m <sup>K19, K21, K24</sup>	82%	81%
C5	K3, K32, K33, K48	74%	65%	m <sup>K3, K32</sup>	79%	76%
C6	K4, K20, K38, K63	68%	68%	m <sup>K4, K38</sup> , d <sup>K20</sup>	86%	86%
C7	K12, K34, K36, K45, K47, K52	76%	70%	d <sup>K47</sup>	84%	80%
C8	K6, K11	77%	77%	-	-	-
C9	K8, K40	83%	79%	m <sup>K8, K40</sup>	94%	92%
C10	K26, K37, K44, K58, K68, K69	66%	65%	m <sup>K26, K68</sup>	73%	71%
C11	K16, K31, K59	83%	79%	-	-	-
C12	K25, K27, K64, K66	71%	58%	m <sup>K27, K66</sup>	77%	77%
C13	K10	78%	77%	-	-	-
C14	K17, K43	88%	84%	-	-	-
C15	K41, K50, K54, K62	94%	90%	-	-	-
C16	K49, K53, K57, K70	89%	82%	m <sup>K57, K70</sup>	91%	87%
C17	K46, K51, K65	97%	95%	-	-	-
C18	K58	92%	91%	-	-	-

849

850 Note: Clusters established by the VA method. Category column shows categories which form the cluster in question. Correct classification

851 marks the percentage of calls correctly classified by the DF analysis into categories belonging to the cluster in question. Merged/discarded

852 column shows merged or discarded categories. Clusters with at least one merged category were reanalyzed by the DF analysis.

853

854

855 **Fig. 1:** Recording Plot

856 Note: Marks denote recording sessions

857 **Fig. 2:** Juruba's repertoire

858 **Fig. 3:** Zoé's repertoire (Giret et al. 2012)

859 **Fig. 4:** Call types performed by both Juruba and Zoé

860 **Table S1:** T-test results

861 Note: Numbers are t-stats, those marked with \* are statistically significant.

862