

Calling rhythm as a predictor of the outcome of vocal interactions: flight departure in pale-winged starling pairs

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1 **Title**

2 **Calling rhythm as a predictor of the outcome of vocal interactions: flight**
3 **departure in pale-winged starling pairs**

4

5

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18

19

20 **Abstract**

21 Vocal communication plays an important role in the regulation of social interactions and
22 the coordination of activities in many animal species. Synchrony is an essential part of the
23 establishment and maintenance of pair bonds, but few reports have investigated decision
24 making at the pair level. We investigated temporal characteristics of call exchanges in pale-
25 winged starlings (*Onychognathus nabouroup*) that could predict whether one, two, or neither
26 members of a pair would take off. Our analysis of these interactions revealed that the overall
27 rhythm of a call exchange, as well as the acceleration towards the end of an interaction, were
28 significantly associated with the type of behavioural outcome. Faster rhythms were associated
29 with higher probabilities that both birds would fly away. Our results confirm the findings of
30 previous studies showing that higher rates of alarm calls indicate imminent departure and
31 highlight the relationship between temporal features of vocal interactions and their outcome.

32

33 **Keywords** decision making, preflight call, vocal interactions, *Sturnids*, *Onychognathus*
34 *nabouroup*,

35

36 **Introduction**

37 Acoustic communication plays a major role in the coordination of activities that are an essential
38 part (Tinbergen 1953) in the social lives of, for example, non-human primates such as *Macaca*
39 *radiata* (Hohmann 1989) and African savannah elephants *Loxodonta africana* (McComb et al.
40 2000). Specific recruitment signals can help conspecifics perceive an emitter's intention to
41 leave (King and Cowlishaw 2009). Different types of acoustic vocal or non-vocal signals
42 associated with group departures in contexts of transition (e.g., from resting to foraging or
43 changing foraging patches) have been described. These include moving calls in meerkats

44 *Suricata suricatta* (Bousquet et al. 2011), piping signals in honeybees *Apis mellifera* (Seeley
45 and Tautz 2001), trills in white-faced capuchins *Cebus capucinus* (Boinsky 1993), flight calls
46 in green wood hoopoes *Phoeniculus purpureus* (Radford 2004) and back glances in both
47 Tonkean macaque *Macaca tonkeana* and rhesus macaques *Macaca mulatta* (Sueur and Petit
48 2010). Group-decision to move away can also be related to arousal-inducing contexts and the
49 alarm calls of different species can induce the departure of group members while giving
50 indications of the type of predator (Zuberbühler 2002; Seyfarth and Cheney 2003) or the nature
51 of the threat (*Sciuridae*: Weary and Kramer 1995; Blumstein and Armitage 1997; Warkentin et
52 al. 2001; primates: Ouattara et al. 2009) via specific call types. Faster call rates indicate the
53 proximity of danger and induce immediate departure in Campbell’s monkeys’ *Cercopithecus*
54 *campbelli* group members (Lemasson et al. 2010). Increased call production is associated with
55 more successful “recruitments” and can be the result of more group members producing calls
56 (e.g., Bousquet et al. 2011; Stewart and Harcourt 1994), accelerated rate of calls by the emitter
57 (Lemasson et al. 2010) or possibly both (Walker et al. 2017).

58 Vocal coordination can be of primary importance. This is shown by “turn-taking” in a variety
59 of species (nightingales *Luscinia megarhynchos* (Naguib 1990), bottlenose dolphins *Tursiops*
60 *truncatus* (Janik 2000); elephants, (Soltis et al. 2005); Campbell’s monkeys (Lemasson et al.
61 2011), white-winged vampire bats *Diaemus youngi* (Carter et al. 2008); naked mole-rats
62 *Heterocephalus glaber* (Yosida et al. 2007)) when the temporal alternation is of primary
63 importance for the outcome of the interaction (e.g., Henry et al. 2015a). The synchronisation of
64 vocalisations can depend upon context (Dahlin and Benedict 2014), revealing some degree of
65 flexibility (Oller and Griebel 2008). While the existence of specific “flight calls” in birds is
66 known, their potential involvement in synchronising departures has rarely been described.
67 Radford (2004) reported that, in wood hoopoes, cackling calls produced during the flight when
68 the emitter moves to a new foraging site announce departure and attract the attention of other

69 group members. However, relatively little is known concerning the role of acoustic signals in
70 decision-making at the pair level, even though synchrony is an essential part of the
71 establishment and maintenance of pair bonds. Females of barnacle geese *Branta leucopsis* can
72 produce vocalisations which inhibit or encourage ritual display in males (Hausberger and Black
73 1990). Ritualised head and neck movements of whooper swan *Cygnus cygnus* and tundra swan
74 *Cygnus columbianus bewickii*, called “pre-flight rituals”, serve as a mechanism for triggering
75 synchronised flight (Black 1988): the rate of signalling increases at the end of a preflight
76 sequence.

77 Considering that the rate of production is a major aspect of the success of specific calls in
78 shared decisions for group departures, we hypothesised that both calling rhythm and synchrony
79 would be a major aspect of pair decision-making for flight departure by monogamous birds. To
80 test this hypothesis, we analysed the temporal features of flight call sequences emitted during
81 within-pair interactions by pale-winged starlings *Onychognathus nabouroup*, a monogamous
82 species with long-living mates. We predicted that acceleration of the rhythm of vocal
83 interactions would signal intent to depart and hence promote simultaneous departure, whereas
84 no acceleration of the slower rhythms would indicate reluctance of one of the partners to depart.
85

86 **Methods**

87 **Study sites and subjects**

88 We studied a resident population of pale-winged starlings in Augrabies Falls National Park,
89 South Africa. These birds are habituated to humans as they feed and rest close to the tourists’
90 accommodations. This species is locally common in the arid regions of south-western Africa,
91 where they breed in monogamous pairs on rocky outcrops (Feare and Craig 1998; Hulley et al.
92 2002). Pale winged starlings’ plumage is sexually monomorphic (Craig and Feare 2009).

93 Accurate sexing requires precise measurements of the tail, wing, tarsus, and culmen as well as
94 their weight after catching (Henry et al. 2015b).

95 The study took place between 2 November and 31 December 2015. The population has
96 been followed since 2011 as a part of a long term comparative project on the evolution of vocal
97 communication in relation to social evolution. Ringing campaigns between 2011 and 2013 led
98 to ringing 87 individuals. Bird ringing was done using small plastic split rings with unique
99 colour combinations. Unfortunately, the colour rings used then did not resist very well the harsh
100 arid climate, and only part of these ringed birds could be easily recognised for behavioural
101 observations. Re-sightings and re-capture made on different fieldwork sessions revealed that
102 these birds show a high site and partner fidelity over years (Lange et al. in prep).

103 Moreover, field observations of pre-flight interactions had to be opportunistic as they
104 are occasional and rather unpredictable events from a human point of view. Thus, the study
105 required that the observer was present before the flight call sequence started, and at a distance
106 allowing proper recording and observation. We opportunistically recorded 43 pre-flight
107 sequences from 18 pairs (9 ringed and 9 unringed) at different locations within the park's
108 residential area, thus ensuring that they were different birds (Lange et al. in prep).

109

110 **Recordings and terminology**

111 A total of 31 hours of song were opportunistically recorded by one observer (MH1)
112 between 6 am and 6 pm. A call sequence was considered to start with the first call produced by
113 either of the birds of the pair and to end by the departure of one or both subjects, a significant
114 change in activity (e.g., to foraging or singing) or a silence lasting more than 10 seconds (i.e.,
115 the maximum interval between two calls in an exchange leading to flight). A departure involved
116 movements of at least several meters and change of location while vertical movements such as
117 landing on the ground or perching on a higher branch were not considered as interrupting the

118 flight call sequence. During recordings, the birds' behaviour and identity of the emitter were
119 recorded. The identity of the emitter was identified based on ring colours when one or both
120 birds were ringed. If one of the birds was not ringed, the first emitter was identified as "A" and
121 the second one as "B". Birds were visually followed until they were out of sight. Vocalisations
122 were recorded on a Marantz PMD 661 MKII recorder (.wav format; sampling rate: 48 kHz;
123 resolution: 16 bit; frequency response 20–20 000 Hz) and with a Sennheiser MKH416-P48U
124 microphone. A sequence was included in the analyses only if the observer was present before
125 the sequence started and there were no other pale-winged starlings within hearing distance.

126 The possible outcomes of a call sequence were recorded as C0: neither bird flew away,
127 and both members of the pair were silent for more than 10s; C1: one of the pair flew away; C2:
128 both birds flew away. We were able to record 43 sequences (13 for C0, 11 for C1 and 19 for
129 C2), 14 of them from unique pairs, recorded only once over the whole recording period (5 for
130 C0, 4 for C1 and 5 for C2).

131

132 **Measurements and statistical analyses**

133 Recordings were analysed using a sound analysis and synthesis software (Richard
134 1991). Sonograms were calculated with an FFT (Fast Fourier Transform) using a 256-points
135 Hanning window and a 128-points step. Sampling frequency was 22 kHz, and pixel size 87 Hz
136 x 11.5 ms. Given the constraints mentioned above (i.e., opportunistic nature of the recordings,
137 rarity of this event, proportion of unringed birds) and because sometimes the birds were not
138 permanently visible due to environmental constraints, we considered each sequence as an
139 independent event (see also Walker et al. 2017). Thus, different pairs were differently
140 represented in the samples, but we controlled for this difference in the statistical models (see
141 below). Moreover, during a call exchange, we were occasionally not able to identify the emitter

142 within a pair, especially when the rhythm increased. Therefore, each pair was introduced in the
143 model as an “individual” and measurements were taken at the sequence level.

144 For each recorded sequence, one of the authors (AG) measured the following
145 parameters: number of calls per sequence, duration of the sequence (sec) and rhythm (number
146 of calls per second). In order to evaluate the potential acceleration of the calling rhythm within
147 a sequence, we divided sequences into three equal parts based on the number of calls in the
148 sequence: “start”, “middle” and “end” (Fig 1). The duration of the first part of the sequence was
149 $X = 19.8 \pm 9.8$ s (range: 2.5 to 49), the duration of the middle part was $X = 19.1 \pm 12.06$ s (range:
150 3.9 to 59), and the duration of the last part was $X = 14.4 \pm 9.9$ s. (range: 2 to 46). We then compared
151 the call rhythm during the first (i.e., “start”) and the last parts (i.e., “end”) of each sequence.
152 We decided to take a similar proportion of the sequence rather than an absolute time because
153 there was a large variability (even within contexts) in the sequences’ durations (from 10.5 sec
154 to 158 sec, $X = 53.24 \pm 27.79$ sec). By taking into consideration the same proportion of time (i.e.,
155 first and last third of sequences), we considered that differences between sequences duration
156 were scaled down.

157 We used an ordered logistic regression to identify which parameters were the best
158 predictors of an outcome. The parameters included in the model were sequence duration,
159 number of calls per sequence, and calls per second. Then we applied a general linear mixed
160 model (GLMM) to test for differences between the rhythm of the first and last parts of
161 sequences according to the behavioural outcome of the pair. In this second analysis, pairs were
162 considered as a random variable and were included as “individual” effects in the model.
163 Normality of residuals was verified using a quantile-quantile plot. Tukey post hoc tests were
164 used to test potential differences in calling rhythms among behavioural outcomes. We also used
165 Tukey post hoc tests to test potential differences between rhythms of the first and last parts of
166 sequences.

167 To test for differences, we performed non-parametric statistics. Changes in rhythm
168 within a sequence according to outcome were estimated by comparing the last (C0:
169 $X=20.5\pm 11.9$, C1: $X=15.8\pm 10.2$, C2: $=9.5\pm 5.1$ sec before the end) and the first parts (C0:
170 $X=17.7\pm 12.9$, C1: $X=21.9\pm 7.6$, C2: $=19.8\pm 8.7$ sec) of a sequence using a Wilcoxon paired test
171 for related samples (Siegel 1956). Statistical significance was set at $p=0.05$. Results are
172 expressed as means and standard error. All statistical analyses were run using R 3.5.3 software
173 (2009) and lme4 package.

174

175

176 **Results**

177 The logistic regression revealed that the number of calls per second was the only
178 parameter that was significantly associated with call sequence outcomes ($\chi^2=4.1$, $df= 1$, $p=.04$).
179 The duration of sequences ($\chi^2=0.61$, $df= 1$, $p=.43$), the number of calls per sequence ($\chi^2=0.53$,
180 $df= 1$, $p= .46$) and the interaction between these two parameters ($\chi^2=0.8$, $df= 1$, $p= .37$) were
181 not associated with a given outcome (Fig 2a, 2b, 2c), (table S1). Likewise, the interactions
182 between number of calls per second and sequence duration ($\chi^2=0.05$, $df= 1$, $p= .8$) and between
183 number of calls per second and number of calls per sequence ($\chi^2=0.02$, $df= 1$, $p= .87$) were not
184 associated with a given outcome.

185

186 The GLMM revealed that the difference in calling rhythms (number of calls per second)
187 between the first part and the last part of a sequence varied with the outcome ($\chi^2=399.01$, $df=1$,
188 $p=10^{-16}$). It also revealed that the calling rhythm globally accelerated during a sequence (Tukey
189 test: $z=15.38$, $p=10^{-16}$). However, outcomes differed according to the overall calling rhythm
190 ($\chi^2=255.26$, $df=2$, $p=10^{-16}$) (Fig 2c), and we found an interaction between the type of outcome
191 and the difference of calling rhythm between the first and the last part of a sequence ($\chi^2=161.48$,

192 $df= 2, p= 10^{-16}$) indicating that modifications of the calling rhythm within a sequence, more
193 precisely the acceleration rate of call rhythm at the end of a sequence (i.e. change between end
194 and start parts) was associated with a given outcome. Thus, no acceleration was found when
195 none of the birds flew away (C0: $W=50, N=12, p=.41$), highly variable but increased rhythm
196 was detected before only one bird left (C1: $W=6=5.5, N=11, p=.01$), and a very consistent
197 increase was detected before both birds departed ($W=3, N=19, p= .00002$) (Fig 3).

198

199 **Discussion**

200 Our analysis of the temporal pattern of pale-winged starling pairs' interactional preflight calling
201 sequences revealed that 1) the overall rhythm of calls was associated with the probability of a
202 pair's departure, i.e., faster rhythms were associated with higher probabilities of departure of
203 both birds, 2) these faster rhythms were mainly due to an acceleration at the end of an
204 interaction, just before departure of the pair. Neither of the members of a pair departed when
205 there was no acceleration. This highlights the fact that calling rhythm is the parameter involved
206 in the outcome of an interaction. This study bridges the gap between movement decision
207 making at the group level, as frequently described in the literature, and decision making at the
208 pair level, more scarcely described.

209

210 Our results are in agreement with previous reports that indicate that faster calling
211 rhythms are associated with higher consensus of movement before groups move off (Ouattara
212 et al. 2009; Stewart and Harcourt 1994). Increased calling rhythm can be achieved by an
213 individual increasing the call rhythm, by a large number of emitters (e.g. Bousquet et al. 2011),
214 or possibly both (Walker et al. 2017). In this study, we could not assess the input of each
215 member of the pair in the acceleration phase. However, the faster calling rhythm observed
216 before departure was probably due to both an individual increase and a greater synchronisation.

217 This hypothesis is supported by the fact that the pattern of sequences preceding departure of a
218 pair is more consistent than the pattern preceding the departure of only one bird. The increased
219 calling rhythm in pale-winged starlings probably reflects the emitter's arousal level in relation
220 to fear, as it has been described for other species (Lemasson et al. 2010) or its arousal due to
221 intended movement (e.g., Stewart and Harcourt 1994) but the level of the receiver's (i.e., mate)
222 response could play a major modulating role on the emitter's vocal production and hence its
223 arousal level and motivation to depart. During "triumph ceremonies", the males of many Anatid
224 species initiate this ritual display and females decide whether or not to join in by alternating
225 calls and displays with their partners (Hausberger and Black 1990; Johnsgard 1962). The older
226 a couple of barnacle geese, the less likely the females are to join in and the more likely they are
227 to produce signals that interrupt the male's display (Bigot et al. 1995). We did not know the
228 ages of the pairs in our study, but this factor may be, apart from other immediate motivational
229 factors, an important aspect that would deserve further investigation.

230 Group decision making studies converge to indicate that a "quorum" has to be reached
231 before an entire group moves off (Sueur and Petit 2008). In meerkats, research has shown that
232 at least 2 or 3 individuals have to emit moving calls before the whole group moves to a new
233 foraging patch (Bousquet et al. 2011). In the case of pair interactions, the mate's reactions
234 constitute the only potential social modulating factor. The fact that a proportion of pale winged
235 starlings' flight call sequences ended without a departure shows that the first emitter's
236 motivation can decrease to the point of renouncing to move. This outcome was associated with
237 an overall slower calling rhythm during the whole sequence, mostly due to the lack of
238 acceleration towards the end of the sequence. Probably, the best explanation is that the weaker
239 responses, and thus less "joining in" of the mate, decreased the emitter's motivation. This
240 decrease in the motivation could have decreased its arousal level and, consequently, calling
241 rhythm, too. Future studies should investigate whether, during a sequence, these birds produce,

242 like barnacle geese, specific vocal signals that inhibit their mates' arousal and related vocal
243 production. The existence of potential inhibitory acoustic signals is a promising line that has
244 been under-investigated and which would demonstrate an active part of the receiver in
245 interrupting the emitter's behaviour. At that stage, the passive inhibitory effect of receivers by
246 "not joining in" vocally (Bousquet et al. 2011; Walker et al. 2017) or spatially (Sueur and Petit
247 2008; Ramseyer et al. 2009; King and Sueur 2011) has been described in a variety of species.
248 The communication behaviours of a few bird species aiming to recruit conspecifics, attract
249 attention, and prevent departure have been previously described. A green wood hoopoe
250 individual that vocalises when leaving its group is significantly more likely to be followed to a
251 new foraging site (Radford 2004). This vocalisation advertises departure and attracts the
252 attention of other group members. Sandhill cranes' *Grus canadensis* pre-flight behaviour leads
253 to coordinated departures (Tacha 1984) as do the pre-flight rituals of whooper swans (Black
254 1988).

255

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264

265 **Compliance with ethical standards**

266 **Conflict of interests** The authors declare that they have no competing interests.

267

268 **Ethical approval** All procedures performed in studies involving animals were in accordance
269 with the ethical standards of the institution or practice at which the studies were conducted.
270 Ethics approval for capture and ringing of birds were granted to Adrian Craig (Rhodes
271 University Ethical Standards Committee, RU-LAD-15-09-0001). Research in the national park
272 and handling of the birds by qualified bird-ringers was approved by the ethical committee of
273 South African National Parks (#HAUM1381).

274

275 **Data accessibility** Data are available in the supplementary electronic material at:
276 <https://doi.org/10.6084/m9.figshare.7448795.v1>

277

278 **Authors' contributions**

279 MH2, LH, MH1, and AC designed the procedure; MH1 performed the field recordings; MH1,
280 LH, MH2, AG, analysed the data; AG, LH, MH2, AC wrote the paper.

281

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285

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370 299

371 **Figure captions**

372

373 **Fig. 1** Sequence of calls (N=36 calls) between 2 ringed birds preceding the flight of both
374 partners (C2 outcome). Each call is noted with the letter of the emitter (A= first emitter,
375 B=second emitter) and a number indicating the order of arrival in the emitter's succession of
376 calls. Triangles indicate the beginning and end of the sequence and the total duration of the
377 whole sequence is indicated at the end (i.e., 40,3 s). The sequence is divided into three equal
378 parts (1/3 = 12 calls) separated here by dotted lines. NA= Calls for which the individual emitter
379 could not be identified.

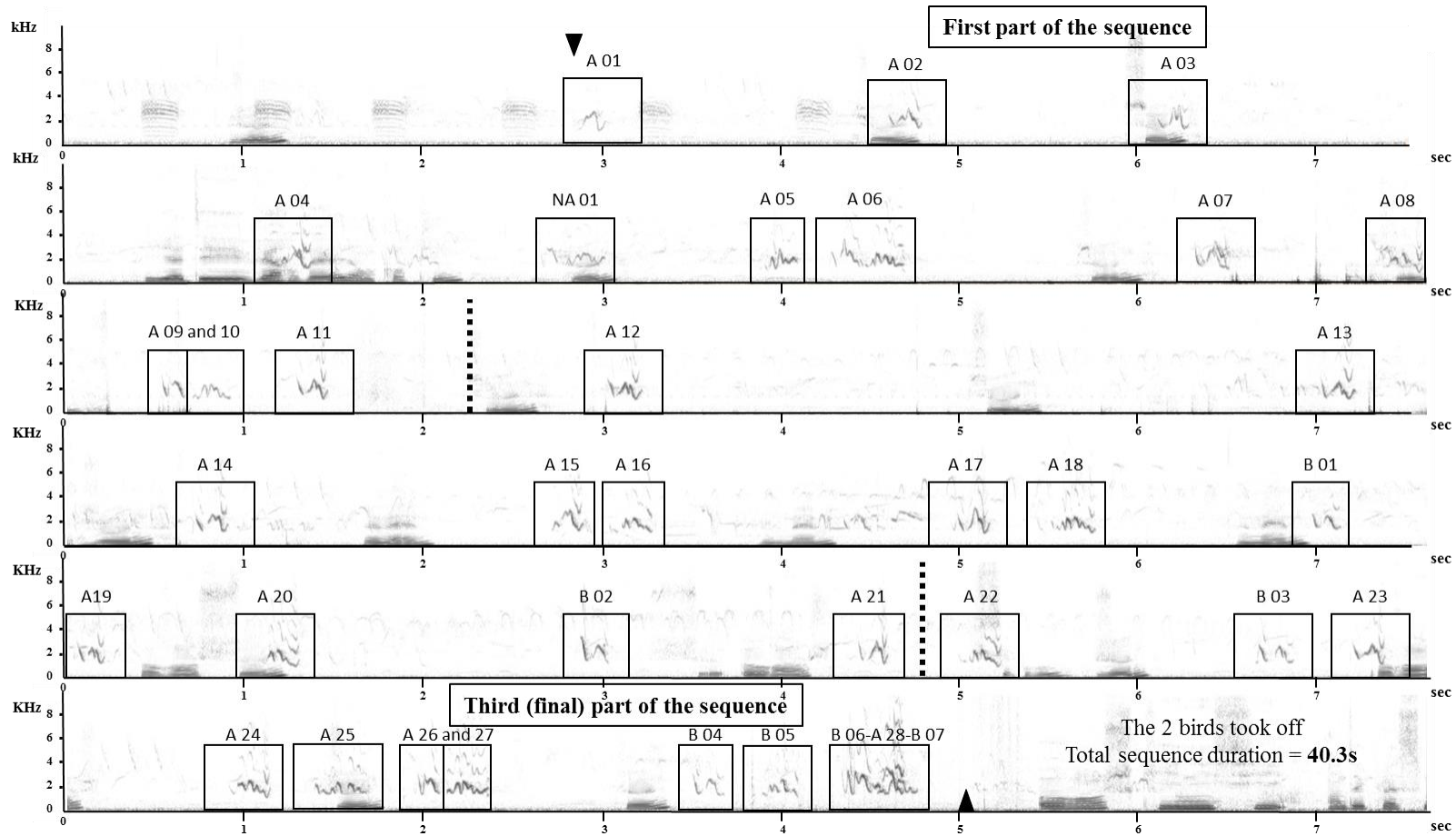
380

381 **Fig. 2** Sequence characteristics. A: Mean duration of sequence according to behavioural
382 outcome. B: mean number of calls per sequence according to behavioural outcome. C: mean
383 number of calls per second, **: $p < .01$

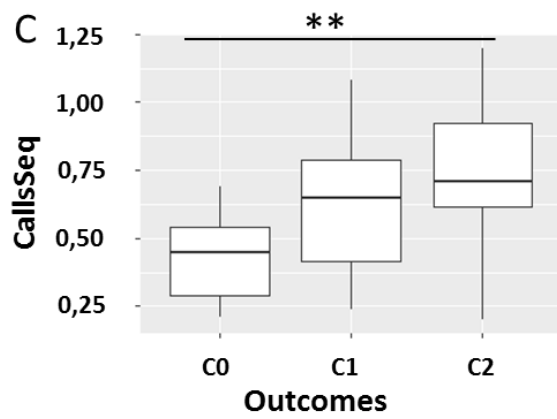
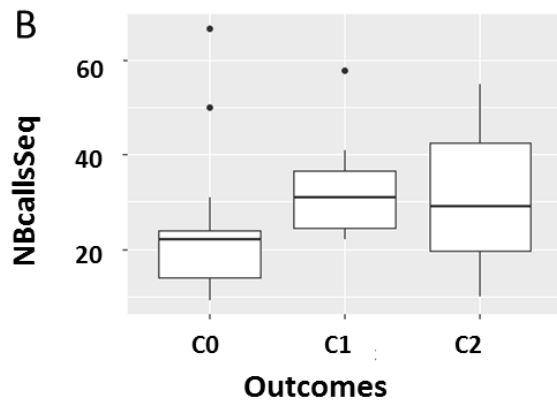
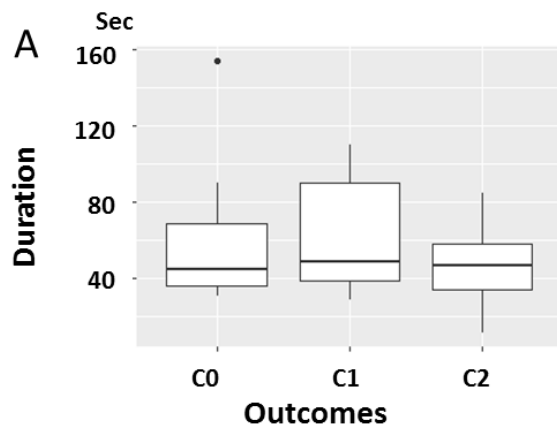
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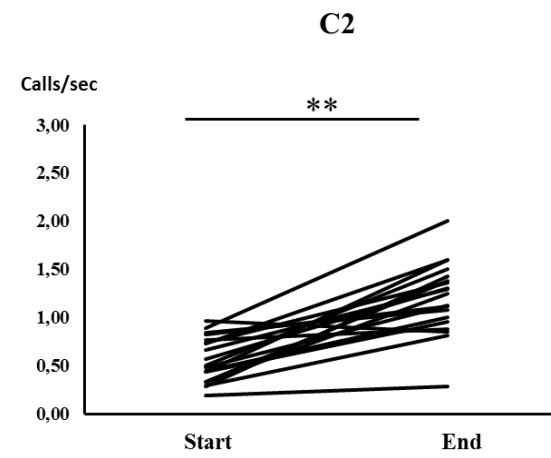
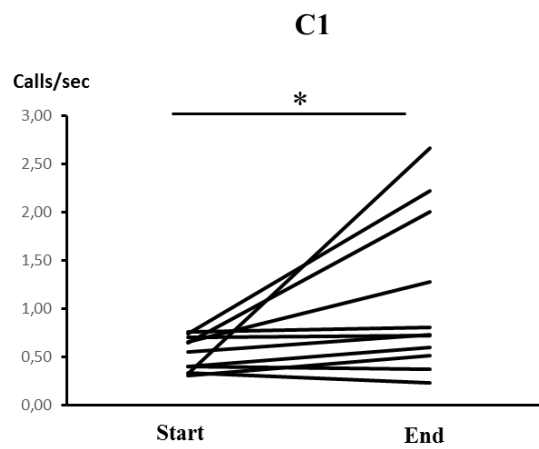
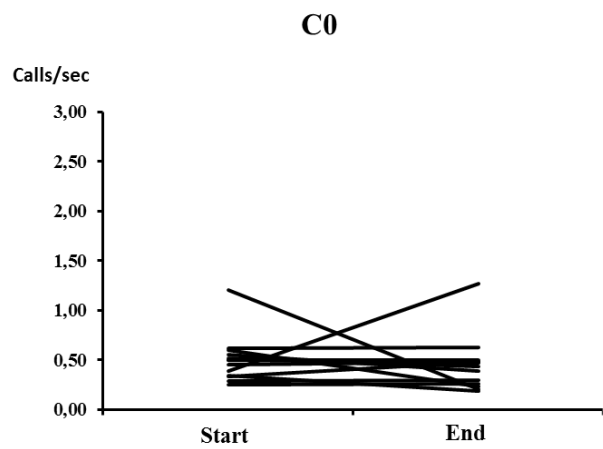
385 **Fig. 3** Changes in the rhythm of a vocal interaction (calls/s) between the “start” and “end” parts
386 of sequences for the three behavioural outcome categories: C0: neither bird flew away, C1: one
387 of the pair flew away, and C2: both birds flew away. Each line represents a different pair.
388 * $p = 0.01$, ** $p = .00001$

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