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

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Title

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Abstract

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

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

Introduction

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

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

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

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

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

Methods

Study sites and subjects

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

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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

Recordings and terminology

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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

5

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

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

Measurements and statistical analyses

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

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

For each recorded sequence, one of the authors (AG) measured the following parameters: number of calls per sequence, duration of the sequence (sec) and rhythm (number of calls per second). In order to evaluate the potential acceleration of the calling rhythm within a sequence, we divided sequences into three equal parts based on the number of calls in the sequence: "start", "middle" and "end" (Fig 1). The duration of the first part of the sequence was X= 19.8±9.8s (range: 2.5 to 49), the duration of the middle part was X=19.1±12.06 s (range: 3.9 to 59), and the duration of the last part was X=14.4±9.9s. (range: 2 to 46). We then compared the call rhythm during the first (i.e., "start") and the last parts (i.e., "end") of each sequence. We decided to take a similar proportion of the sequence rather than an absolute time because there was a large variability (even within contexts) in the sequences' durations (from 10.5 sec to 158 sec, X=53.24±27,79 sec). By taking into consideration the same proportion of time (i.e., first and last third of sequences), we considered that differences between sequences duration were scaled down.

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

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

Results

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

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

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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).

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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.

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

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

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

Compliance with ethical standards

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

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

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

Authors' contributions

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

References

Bigot E, Hausberger M, Black, JM (1995) Exuberant youth: the example of triumph ceremonies in barnacle geese (*Branta leucopsis*). Ethol Ecol Evol 7: 79-85. 37

Black JM (1988) Preflight signalling in swans: a mechanism for group cohesion and flock formation. Ethology **79**: 143-157

Blumstein DT, Armitage KB (1997) Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. Anim Behav 53: 143-171

Boinsky S (1993) Vocal Coordination of Troop Movement Among White-Faced Capuchin Monkeys, *Cebus capucinus.* Am J Prim 30: 85-100

Bousquet CAH, Sumpter DJT, Manser MB (2011) Moving calls: a vocal mechanism underlying quorum decisions in cohesive groups. Proc. R. Soc. B 278: 1482-1488.

Carter GG, Skowronski MD, Faure PA, Fenton B (2008) Antiphonal calling allows individual discrimination in white-winged vampire bats. Anim Behav 76: 1343-1355

Craig AJFK, Feare, CJ (2009) Familiy Sturnidae (starlings). In: Del Hoyo J, Elliott A, Christie D (eds) Handbook of the birds of the world, Vol. 14, Barcelona: Lynx Editions, pp. 654-758

Dahlin CR, Benedict L (2014) Angry birds need not apply: a perspective on the flexible form and multifunctionality of avian vocal duets. Ethology 120: 1-10

Feare C, Craig AJFK (1998) Starlings and mynas. London, A & C Black.

Hausberger M, Black JM (1990) Do females turn males on and off in barnacle goose social display? Ethology 84: 232-238

Henry L, Craig, AJFK, Lemasson A, Hausberger M (2015a) Social coordination in animal vocal interactions. Is there any evidence of turn-taking? The starling as an animal model. Front Psychol 6: 325–328.

Henry L, Biquand V, Craig AJFK, Hausberger M (2015b) Sexing adult pale-winged starlings using morphometric and discriminant function analysis. PLoS ONE, 10 (9), pp.e0135628.

Hohmann G (1989) Vocal communication of wild bonnet macaques (*Macaca radiata*). Primates 30: 325-345

Hulley PE, Craig AJFK, Walter GH (2002) Group displays in pale-winged starlings. Afr Zool 37: 105-107.

Janik VM (2000) Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289: 1355-1357

Johnsgard PA (1962) Evolutionary trends in the behavior and morphology of the Anatidae, Wildfowl 13: 340, 130-148

King AJ, Cowlishaw G (2009) Leaders, followers, and group decision-making. Communicative & Integrative Biology 2: 147-150.

King AJ, Sueur C (2011) Where next? Group coordination and collective decision making by primates. Int. J. Primatol 3: 1245-1267

Lemasson A, Glas L, Barbu S, Lacroix A, Guilloux M, Remeuf K, Koda H (2011) Youngsters do not pay attention to conversational rules: also in nonhuman primates? Sci Rep 1: 22.

Lemasson A, Ouattara K, Bouchet H, Zuberbühler K (2010) Speed of call delivery is related to context and caller identity in Campbell's monkey males. Naturwissenschaften 97: 1023-1027.

McComb K, Moss C, Sayialel S, Baker L (2000) Unusually extensive networks of vocal recognition in African elephants. Anim Behav 59: 1103-1109

Naguib M (1990) Effects of song overlapping and alternating in nocturnally singing nightingales. Anim Behav 88: 1061-1067

Oller K, Griebel, U (2008) Evolution of communicative flexibility: Complexity, creativity, and adaptability in human and animal communication. Cambridge, MA, MIT Press.

Ouattara K, Zuberbühler K, N'goran EK, Gombert JE, Lemasson A (2009) The alarm call system of female Campbell's monkeys. Anim Behav 78: 35-44

R Development Core Team, R: a language and environment for statistical computing, 2009 Vienna Austria) R Foundation for Statistical Computing ISBN 3-900051-07-0 Available from: http://www.R-project.org/

Radford AN (2004) Vocal coordination of group movement by green wood hoopoes (*Phoeniculus purpureus*). Ethology 110: 11-20

340   Ramseyer A, Petit O, Thierry B (2009) Decision-making in group departures of female

341   domestic geese. Behaviour 146: 351-371

342   Richard JP (1991) Sound analysis and synthesis using an Amiga microcomputer. Bioacoustics

343   3: 45-60

344   Seeley T, Tautz J (2001) Worker piping in honey bee swarms and its role in preparing for liftoff.

345   J Comp Physiol 187: 667-676.

346   Seyfarth RM, Cheney DL (2003) Meaning and emotion in animal vocalizations. Ann NY Acad

347   Sci 1000: 32–55

348   Siegel S (1956) Nonparametric statistics for the behavioural sciences. McGraw-Hill,

349   Kogakusha, Ltd.

350   Soltis J, Leong K, Savage A (2005) African elephant vocal communication I: antiphonal calling

351   behaviour among affiliated females. Anim Behav 70: 579-587

352   Stewart KJ, Harcourt AH (1994) Gorillas' Vocalizations During Rest Periods: Signals of

353   Impending Departure? Behaviour 130(1):29-40

354   Sueur J, Petit O (2008) Shared or unshared consensus decision in macaques? Behav Processes.

355   78: 84-92

356   Sueur C, Petit O (2010) Signals use by leaders in *Macaca tonkeana* and *Macaca mulatta*: group-

357   mate recruitment and behaviour monitoring. Anim Cogn 13: 239–248

358   Tacha, T.C. (1984) Preflight behavior of sandhill cranes. Wilson Bulletin 96: 471-477

359   Tinbergen N (1953) Social Behaviour in Animals. Chapman and Hall, London.

360   Walker RH, King AJ, McNutt JW, Jordan NR (2017) Sneeze to leave: African wild dogs

361   (Lycaon pictus) use variable quorum thresholds facilitated by sneezes in collective decisions.

362   Proc R Soc B 284: 20170347

363   Warkentin KJ, Keeley AT, Hare JF (2001) Repetitive calls of juvenile Richardson's ground

364   squirrels (*Spermophilus richardsonii*) communicate response urgency. Can J Zool 79: 569-573

365 Weary DM, Kramer DL (1995) Response of eastern chipmunks to conspecific alarm calls.

366 Anim Behav 49: 81-93

367 Yosida S, Kobayasi KI, Ikebuchi M, Ozaki R, Okanoya K (2007) Antiphonal Vocalization of a

368 Subterranean Rodent, the Naked Mole-Rat (*Heterocephalus glaber*). Ethology 113: 703-710
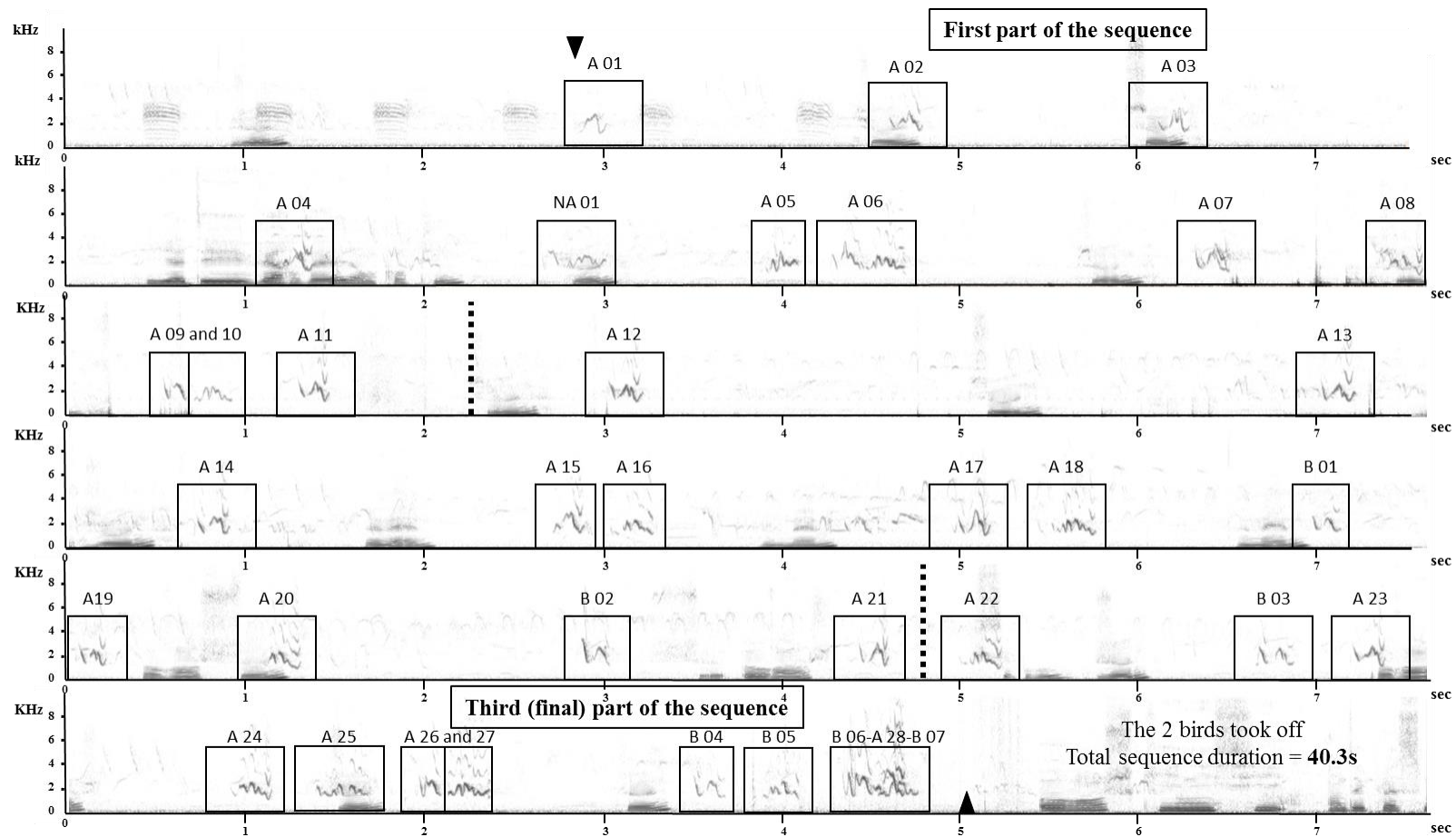
369 Zuberbühler K (2002) A syntactic rule in forest monkey communication. Anim Behav 63: 293-
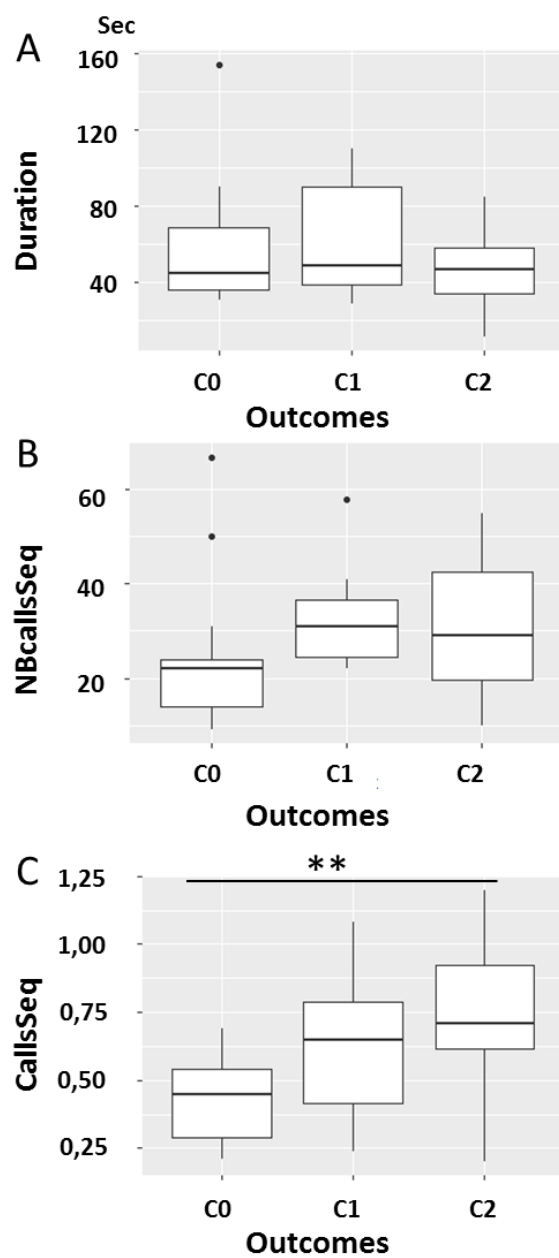
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Figure captions

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

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

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

First part of the sequence

Third (final) part of the sequence

The 2 birds took off
Total sequence duration = **40.3s**

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