

Original Article

Temporal patterns of broadcast calls in the corncrake encode information arbitrarily

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By combining different vocalizations, in different ways, animals have the potential to vastly increase the range of information that can be encoded in acoustic signals. Although such a mechanism is hard to apply in species having small repertoires, individuals can increase the amount of information by separating vocalizations with intervals of different length, that is, with vocalizations functioning as commas and intervals as carriers of information. Nevertheless, there has been little study of information encoding using temporal arrangement of single call types. We have recently shown that male corncrakes (*Crex crex*) produce such temporal patterns in correlation to their aggressive motivation and these elicit the according behavior in the receivers. In this study, we report that the design of these patterns is arbitrarily related to their function. The aggressive information is encoded in the syntactic pattern itself, not in the absolute length of intervals, and thus signal variants appear to transfer different kinds of information without any association with the structure of signal variants. The finding of such coding in acoustic signaling in species with innately programmed call structures implies a much larger flexibility and complexity of communication systems of animals in general and in species with low repertoires of genetically coded vocalizations in particular. *Key words*: coding scheme, conventional communication, corncrake, *Crex crex*, signal function. [*Behav Ecol*]

INTRODUCTION

One of the most striking characteristics of communication systems of animals is the functional relationship between the form of the signal and information transferred (Clarke et al. 2006). In other words, there are practical reasons why a signal transfers one kind of information but not the other. For example, the constraints on vocal production mechanisms make some signal types more challenging to produce, for example, rapidly repeated syllables (Podos 1997) or highly synchronous duetting in birds (Hall and Magrath 2007), and therefore more likely to transfer a more salient information. Others, as so-called indices (Maynard Smith and Harper 2003), for example, calls with the low dominant frequency in frogs (Wagner 1989) or groans with low fundamental frequency and low formant dispersion in deers (Vannoni and McElligott 2008), are honest correlates of physical attributes of senders, in which a signal's meaning is associated with its method of production (Hingee and Magrath 2009). In contrast, some communication systems, as for example, human language, are, for the most part, based on conventions (so-called conventional signals), in which the association between the form of the signal and information transferred is arbitrary, being a consequence of an agreement between the sender and receiver (Guilford and Dawkins 1995; Tomasello 2008).

From the evolutionary perspective, any constraint on the arbitrariness of the signal can play a role in the maintenance of the reliability of the signal and consequently affect the function of the signal (Guilford and Dawkins 1995; Gil and Gahr 2002; Maynard Smith and Harper 2003). It is because, constraints on arbitrariness can play the role of hidden costs

maintaining the reliability of signals and thus influencing the function of signals, for example, making some signal variants available only to a specific fraction of individuals. Because conventional signals are not causally or functionally constrained (Lachmann et al. 2001; Hurd and Enquist 2005), they are vulnerable to deception if the interests of the sender and receiver are opposed (e.g., during aggressive interactions or courtship) (Searcy and Nowicki 2005). They therefore require social mechanisms that act to counter deception (e.g., receiver retaliation) (Számadó 2010). Consequently, studying the constraints on the arbitrariness of signals is a key issue for understanding the evolution of animal communication (Maynard Smith and Harper 2003; Hurd and Enquist 2005).

Except for humans, acoustic conventional signals have been also hypothesized in birds, including song-type matching and switching rate, singing strategies serving as effective long distance threat signals in songbirds, for example, in the banded wren (*Thryothorus pleurostictus*) and song sparrow (*Melospiza melodia*) (Molles and Vehrencamp 2001; Vehrencamp 2001). However, recent evidence suggests that there are functional reasons (constraints on the arbitrariness) why a match is a more salient signal than a nonmatch and why switching at different rates means different levels of engagement (Collins 2004; Logue and Forstmeier, 2008; Bradbury and Vehrencamp 2011; Jordan and Yuan 2011). Matching allows males to better compare each other's song quality while performing the same song type and switching rate (either lower or higher) aims at producing an antithetical signal to the signal of the opponent. Immediate variety singers like banded wrens can only reduce switching during aggressive encounters, whereas bout singers like song sparrows can only increase switching during aggressive encounters. More recently it was reasoned that the temporal arrangement of syllables within the call of the corncrake (*Crex crex*) is an example of a specific conventional system based on syntax (Ręć and Osiejuk 2010). This system is equivalent

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to a very simple Morse code, in which the information about male's aggressive motivation is encoded in sequences of similar vocalizations and intervals of variable length (so-called rhythm—see Methods for definition; Figure 1). Previous experiments, testing reactions of males to natural calls, calls with artificial intervals, and calls with artificial syllables, ruled out the possibility that calling rhythms are byproducts of body size, structural call parameters, or male identity on responses, and it indicated that males react similarly to the patterns with natural and artificial ratios of intervals and to the patterns with consistent and inconsistent intervals (Ręk and Osiejuk 2010). Because of its simplicity, this system is an especially good model for studying coding schemes in acoustic signals.

Corncrake males produce very loud broadcast (heard >1 km) calls (synonym for cracking call) nearly continuously throughout most of the night at a high rate. Individual calls consist of 2 syllables (S1 and S2) separated by 2 intervals (I1 and I2). S2 is usually slightly longer than S1, but both syllables are acoustically identical. When subsequent intervals have similar lengths the calling sounds monotonous, when short intervals (I1) alternate with long intervals (I2) the calling sounds intermittent. Such variation constitutes a graded aggressive signal with syllables given at less regular intervals (more intermittently) by males behaving more aggressively. Intermittent calling also elicits more aggressive responses (Ręk and Osiejuk 2010). Such signaling appears to have conventional character because higher aggressive motivation is communicated by a signal with a lower rate of syllables (a signal with a supposedly lower production cost) than lower aggressive motivation, and the honesty of this signal is maintained by a receiver retaliation cost rather than by production costs (Ręk and Osiejuk 2010). At the same time, males can call with either pattern for very long time (Osiejuk et al. 2004), which suggests that neither pattern is harder to produce and to maintain.

The question we ask here is, why the intermittent pattern is the more aggressive signal and the monotonous one the more submissive or less aggressive signal? On the one hand, the production of intermittent versus monotonous pattern could be functionally constrained in a similar way as song-type matching or switching rate in songbirds (constraint hypothesis). For example, calling with the regular monotonous pattern might mean a male is just advertising for females or territory ownership without wanting to interact aggressively (leaving short silent gaps and ignoring any replies), whereas the intermittent pattern might mean the male is leaving a silent gap to listen for replies from other males and “inviting” aggressive countercalling. This option is not the only one by which the temporal pattern of the signal could be nonarbitrary, but our reasoning is that any functional (nonarbitrary) use of this spacing pattern should be associated with the sensitivity of receivers to the absolute length of call intervals, not the pattern itself. On the other hand, there could be no practical reason why leaving alternately short and long pauses between syllables signals greater aggressive tendencies (no-constraint hypothesis). In this case, it is the arbitrary pattern itself (relative organization of syllables and intervals) that receivers should respond to. To test between these 2 hypotheses, we presented male corncrakes with playbacks including natural intermittent rhythm (NAP) of calls and its modified artificial versions (AP) having the same maximal lengths of intervals but monotonous rhythm (Figure 1). If the aggressive information is encoded in the maximum spacing between the separate waveforms (in the absolute length of intervals or in the length of the longer interval [I2]), males should respond with similar or higher intensity to AP than to NAP. This would imply that a change from a monotonous to an intermittent rhythm has a strictly functional basis. If the longer intervals do not play any functional role, males should respond with

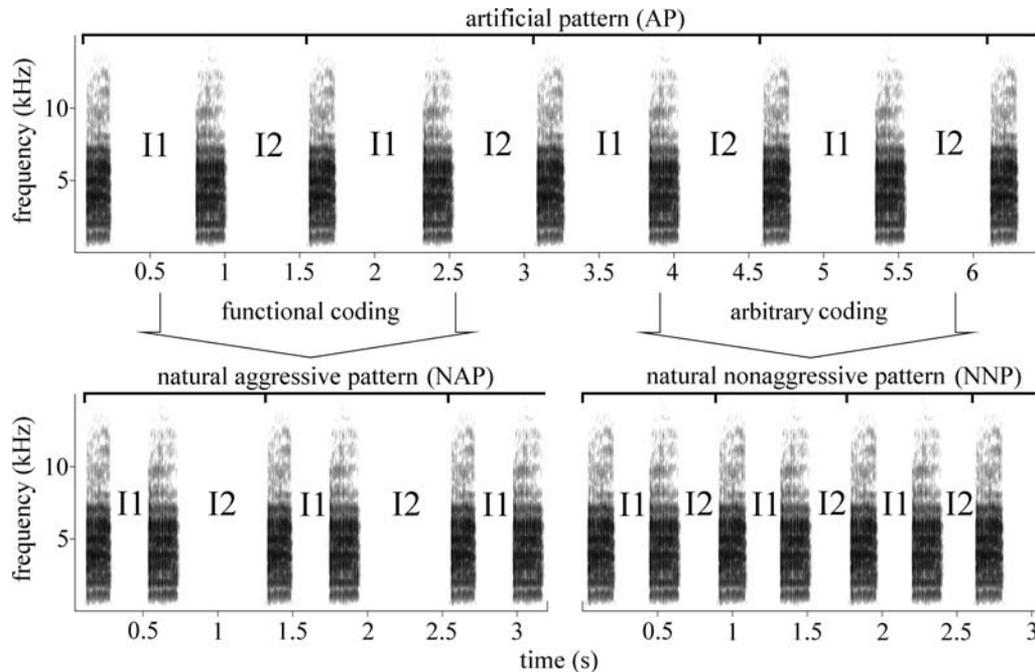


Figure 1

The hypothetical meaning of the artificial pattern depending on the coding scheme of information within corncrake calls. Arrows indicate encoding rules that must have been involved in order for the artificial pattern to be understood as aggressive or nonaggressive signal. In the case of functional coding (constraint hypothesis), the information should be encoded in the absolute length of intervals (length of I1 + I2; AP stronger than NAP, NAP stronger than NNP) or in the maximal length of the interval (length of I2; AP equivalent to NAP, AP and NAP stronger than NNP). In arbitrary coding (no-constraint hypothesis), the information should be encoded in the relative length of intervals, for example, in I1/I2 ratio (AP equivalent to NNP and weaker than NAP).

significantly lower intensity to AP than to NAP. This would imply that the aggressive information is encoded in the ratio of I1 to I2 or equivalently in the relative temporal organization of syllables (the pattern itself), not in the absolute length of intervals (Figure 1), and that the difference between the information transferred by intermittent and monotonous patterns is not functionally constrained by signal structure.

METHODS

Study site and species

The study was carried out in Kampinoski NP in Poland (20°23'E and 52°19'N), 15–22 May of 2011. The subjects were 24 territorial corncrake males, randomly selected from a larger population. Males aggregate in widely spaced clusters (distance to the nearest neighbor in 2010 in the same area: mean \pm SE = 363.08 \pm 73.52 m) and call almost continually throughout the night. Therefore, they are rarely isolated acoustically from their neighbors. Nevertheless, the fact that males respond to playback only in relatively short distances of <50–100 m (Ręk and Osiejuk 2010) suggests that the effect of neighbors' calling on the responses of subject males was irrelevant.

The study was conducted in the time of territory establishment by males, that is when males call the most intensively, attracting females that arrive to breeding grounds a few days later than males (Green et al. 1997). Hence, it was the time of the strongest and most aggressive competition between males. Because males do not sing immediately after the arrival and they sing infrequently during a period of close association with females (Tyler and Green 1996; Green et al. 1997), singing activity is a good indicator of male's breeding stage (Osiejuk et al. 2004). Nevertheless, despite males being able to call from the very similar position even for weeks, their movements, possible mortality, and reproductive performance make estimates of the average number of calling nights unreliable. Circumstantial evidence suggests that broadcast calls share both functions: to repulse other males and to attract females. However, we are not aware of any experiments testing whether females differentiate between monotonous and intermittent rhythms.

Preparation of call stimuli and playback protocol

Calls for playbacks were recorded from 48 different males in 2009 about 250 km northeast from the study area and digitized using the Avisoft SASLab Pro 4.52 sound analysis package (48 kHz/16-bit PCM files). Each playback sample was prepared to match a 96 \pm 5 dB (sound pressure level [SPL] at 1 m) (natural level—mean: 96 dB, range 80–101 dB). Trials were carried out between 2200 and 0215 h local time, which corresponds with the peak of nocturnal vocal activity of corncrakes. Playback calls were broadcast through the amplified loudspeaker (20 W, frequency range 50–15 000 Hz; SEKAKU WA-320) connected to a Creative ZEN player.

Each trial used a different set of calls belonging to 2 kinds of stimuli (Figure 1): 1) natural calls with intermittent rhythm (natural aggressive pattern [NAP]) and 2) artificial calls (artificial pattern [AP]). Call rhythm was defined as the ratio "I2/(S1 + I1 + S2)" (I1 = interval 1, S1 = syllable 1, I2 = interval 2, S2 = syllable 2; Figure 1). To avoid the potential confounding effect of the rhythm, we selected the calls with a similar rhythm (mean: 0.83, range: 0.81–0.87; ca. natural range: 0.4–1.3). AP calls were prepared based on NAP calls used in the same trial through the lengthening of I1s to the length of I2s. As a result, the absolute length of intervals in AP was even longer than in NAP (the maximal lengths of

intervals in AP and NAP were the same), whereas the calling pattern of AP was monotonous, the same as the pattern of natural nonaggressive calls (NNP) (Figure 1). The calls used in each trial came from a single male. Both stimuli were organized into six 20-s sections (3 NAP sections for 20 s each and 3 AP sections for 20 s each) and played in random order for each subject, alternately with 10-s silent sections (e.g.: AP [20 s], silence [10 s]; NAP [20 s], silence [10 s]; NAP [20 s], silence [10 s]; AP [20 s], silence [10 s]; NAP [20 s], silence [10 s]; AP [20 s], silence [10 s]). Each trial lasted 180 s including 10-s interval after the last playback. To exclude the possibility that by playing AP recordings we created merely a very low-quality submissive stimulus, we compared the responses of 24 males to AP and NAP tested in 2011 with responses of males tested in 2007–2008 to NAP and NNP. The 36 trials from a paired design experiment, conducted in 2007–2008 in the same location, tested the responses of 18 males to 2 playback stimuli: NAP and NNP. Because the same methodology was used in the present and previous experiments, the results could be directly compared.

Before each trial the loudspeaker was placed <0.5 m above the ground, within the subject male's territory (distance between the speaker and male: mean \pm SE = 13.0 \pm 1.48). Trials were conducted within an acoustic location system (ALS), which consisted of an array of 4 omni-directional microphones (Sennheiser K6/ME 62) recording to an Edirol R-4 Pro 4-channel Portable Recorder and Wave Editor (Hamamatsu, Japan). We used the acoustic locator algorithm in XBAT (v. 0.6.1, Cornell Lab of Ornithology) to determine the position of focal subjects within the microphone array; however, we considered only the positions measured during silent sections (before, during, and after the trial).

Data analysis and statistics

The use of a microphone array for objective measurement of subjects' positions and movements (ALS) represents an important improvement over the more typical visual estimates because it enables continual record of an individual's behavior during the trial. Traditional estimates, as for example: the change of the distance to the speaker, the number of attacks, the delay to attack, or the time spent close to the speaker together seem to convey a significant amount of information about a male's intentions, but separately they only partially convey the picture of responses. In order to make use of the data from the ALS, we used an index that quantifies comprehensively a male's behavior throughout the trial, that is mode of approach (MA). This index enables the quantification of such complex behaviors like, for example, encircling and it is a strong predictor of the number of attacks (Ręk and Osiejuk 2010). Its suitability was assessed in this species and it was proved that the pattern it describes is not artificially generated by the transformation of the original data (Ręk and Osiejuk 2010). MA is given by the formula:

$$MA = \frac{1}{4} \sum_{s=0}^3 \left[\arccos \left(\frac{d_b - d_a}{d_r} \right) \times \log_9 d_a \right]$$

for both NAP and AP playbacks, where s = silent sections (0 = before the first playback of a given type [NAP or AP] or before the trial if a given recording was played as first; 1–3 = during silent sections, after 3 playbacks of a given type [NAP or AP]), d_b = distance to the speaker before the playback of a given type, d_a = distance to the speaker after the playback of a given type, and d_r = the real distance covered. The arccos function transforms the distance measures (d) into the angle of approach, in such a way that the more

direct approach toward the speaker, the smaller the angle. Consequently, a male approaching the speaker directly would have $MA \approx 0$. A mode of approach of 90 is critical because it means a bird stands still or moves along the radius (distance to the speaker) and values lower or higher mean a bird moves toward or away from the speaker, respectively. In addition, this measure includes a correction (weight) for distance ($\log_9 d_n$) that is important because of some restrictions to motion during playback experiments (Ręk and Osiejuk 2010). First, before the analysis of recordings, the subjects' initial distance from the speaker was unknown. Second, males that approached the speaker closely could not come further, and if, for example, they approached the speaker fast during the first-time section and later moved slightly back or sideways, the average direction would suggest that the male moved away from the speaker. By correcting for distance, the MA of a subject that was far from the speaker and moved outward decreased much more than the MA of a bird that was closer and moved outward. Conversely, if a bird was close to the speaker and moved some distance inward, its MA increased more than that of a bird moving the same distance inward but from a further position. Consequently, the MA values from consecutive silent sections were calculated with reference to specific current circumstances and did not affect each other. The base of the logarithm (here we used 9) determines the critical distance below and above which the mode of approach of males started to increase and decrease, respectively. We chose this value because it minimizes the skewness of the MA distribution.

Except for MA, we used the second behavioral measure that comes directly from observation—first attack, which defines the section (AP or NAP) of male's first attack on the speaker during the trial. Because the same number of trials started from AP and NAP playbacks, first attack enabled us to differentiate the responses of subject males to experimental playbacks from side effects of specific experimental circumstances (presence of people, etc.). To analyze this binary distributed variable, we used generalized linear mixed models (GLMMs), with the male used as subject variable and playback (AP and NAP) as within subject variable. All statistics were calculated in SPSS v20.0.

RESULTS

Males approached the playback speaker significantly faster and more closely (lower mode of approach score) during NAP playback sections than during AP playback sections (NAP_{2011} mean \pm SE = 54.55 ± 11.09 , AP_{2011} mean \pm SE = 69.90 ± 11.32 , Wilcoxon matched pairs test: $Z = 2.62$, $P = 0.009$; Figure 2), despite travelling similar distances during both playback sections (NAP_{2011} mean \pm SE = 1.77 ± 0.30 m/40 s, AP_{2011} mean \pm SE = 1.76 ± 0.31 m/40 s, Wilcoxon matched pairs test: $Z = 0.03$, $P = 0.976$). Furthermore, from among 9 attacking males, 8 males attacked the speaker for the first time during NAP section and only 1 male attacked the speaker for the first time during AP section (GLMM: $F_{1,46} = 4.64$, $P = 0.036$). These differences support the no-constraint hypothesis.

As expected, the comparison of the MA scores of 24 males to AP and NAP tested in 2011 with scores of 18 males tested in 2007–2008 to NAP (NAP_{2007} mean \pm SE = 52.39 ± 8.01) and NNP (NNP_{2007} mean \pm SE = 65.74 ± 1.02) showed similar responses of males in both periods to NAP (NAP_{2007} – NAP_{2011} , Mann–Whitney U test: $U = 202$, $P = 0.722$; Figure 2) and, in agreement with the no-constraint hypothesis and against the constraint hypothesis, similar responses to NNP and AP (NNP_{2007} – AP_{2011} , $U = 215$, $P = 0.980$; Figure 2).

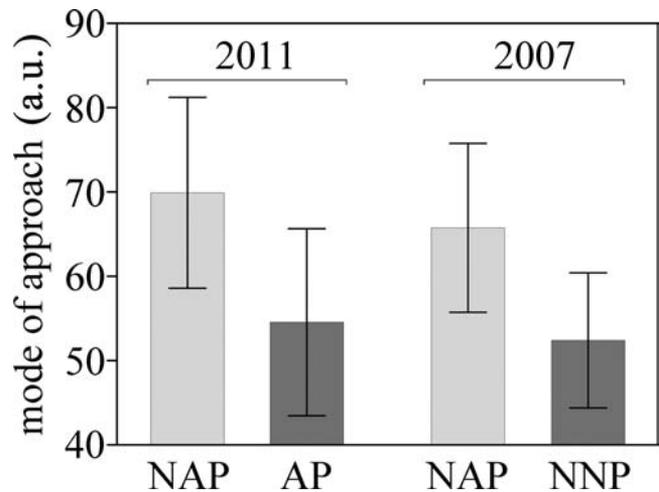


Figure 2

The variability of males' responses to artificial playbacks (AP), natural aggressive playbacks (NAP), and natural nonaggressive playbacks (NNP). Lower values of mode of approach score indicate stronger reactions. a.u., arbitrary units ~ degrees.

DISCUSSION

The results of the present experiment suggest that an increase of the length of I2, and consequently a change from one calling pattern to another, is not functionally constrained but it acts as an arbitrary system of information encoding. In other words, this result points to the pattern, not the absolute length of intervals, being critically important in coding of information in corncrake's calls. Present research opposes an option that has been stated in previous research (Ręk and Osiejuk 2010), but not tested yet explicitly: that changes in calling pattern might instead facilitate localization of rivals. It also verifies the hypothesis that the signal is dependent on the relative lengths of intervals or relative temporal organization of syllables, supporting the idea that the calling patterns in the corncrake are truly arbitrary conventional signals. Consequently, this article provides an important resolution to a controversial question, namely whether animal signals produced during aggressive interactions can provide information about sender's motivation using an arbitrary coding scheme, where the only mechanism maintaining the reliability of the signal is the risk of receiver retaliation (Enquist 1985; Zahavi 1993; Vehrencamp 2001; Maynard Smith and Harper 2003; Searcy and Nowicki 2005).

Although we cannot exclude the possibility that other factors besides the temporal arrangement of syllables could influence the responses of males, our results support our previous work suggesting that calling rhythm in the corncrake is a conventional signal (Ręk and Osiejuk 2010, 2011) and definitely support the predictions expected for a conventional signal (Guilford and Dawkins 1995). One of the best substantiated alternative hypothesis concerning the use and the evolution of various types of vocalizations, their structure, and delivery pattern to make "words and phrases" is to enable birds to negotiate boundary disputes (Loher and Dambach 1989). Nevertheless, it appears very unlikely that a change of rhythm from monotonous to intermittent has anything in common with listening to rivals and negotiating territory boundaries and there are several arguments against it. Firstly, while changing rhythm from monotonous to intermittent one, males extend only I2, keeping I1 constant (Osiejuk et al. 2004). At the same time, they make long and irregular intervals between syllables (a few seconds) when

disturbed (Ręk and Osiejuk, unpublished data), which seems to be a behavior truly associated with listening. Secondly, rhythm is remarkably regular, whereas interactions are not. Males approaching one another modify rhythm, but there are no abrupt transitions, which might be expected from countercalling and aggressively interacting opponents. Moreover, because syllables of different individuals differ in length (intra-individual variability is small) and the length of I1 is strongly correlated with S1 (Osiejuk et al. 2004), overlapping or masking of calls of opponents is practically impossible. Thirdly, because later in the season most of males call monotonously (Osiejuk et al. 2004), rhythm is of no use to receivers in distinguishing the calling of senders from a more harmonic noise. Finally, the recent findings indicated that the blockage of testosterone action suppresses aggressive behaviors of males, but it does not affect their rhythm of calling, suggesting that rhythm is not hormonically linked with aggressive behaviors but it is rather under direct control of the neural system (Ręk et al. 2011). Consequently, a male has a potential for free and fast changes of the signal, which are not constrained by some causal mechanism.

Corncrake belongs to the rallidae family, a cosmopolitan but quite homogenous group of small- to medium-sized birds, associated mostly with wetlands and dense vegetation. Because a majority of rail species are highly territorial and vocally active at night, much of their communication appears to be based on acoustic signals. This observation contrasts, however, with relatively small repertoires of their calls (Cramp and Simmons 1980). Perhaps the most striking shared feature of the rail communication systems is the presence of 1 or a few similar loud call types produced in long series (even more than a thousand in a single bout), but with variable temporal and structural organizations. Such repetitive calling resembles simple trills of songbirds or highly repetitive calling in amphibians or orthopterans (Gerhardt and Huber 2002), which superficially appears redundant; however, it can be a source of the unlimited number of temporal combinations creating many possibilities for information encoding (Yip 2006; Hailman 2008).

The problem of the information content of vocalization arrangements compared with the information conveyed by separate elements has been extensively debated among primatologists studying vocal semantics and ornithologists studying the diversity and temporal organization of basic units building songs (Freeberg and Lucas 2002; Ouattara et al. 2009; Van Heijningen et al. 2009). Conversely, there has been little study of information encoding using temporal arrangement on single call types (Evans et al. 1993; Schehka et al. 2007). In such systems, the size of the repertoire of vocalizations is not a constraint on the diversity of signals (Hailman 2008). Although temporal arrangement of vocalizations is not the sole scheme of acoustic coding in nonlearning birds, substantiated alternatives, such as the shifts of frequency or amplitude within vocalizations (Hardouin et al. 2007; Janicke et al. 2008; Cardoso 2012), are costly measurements of vocal performance, limited by motor constraints similar to those in vocalizations of learning birds (Podos 1997). Therefore, the present results suggest a much larger flexibility and complexity of communication systems in species with small repertoires of nonlearned vocalizations, that is, where signalers have limited ability to modify the structure of their calls into new call types.

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