Sophistication and simplicity: conventional communication in a rudimentary system

Paweł Ręk and Tomasz S. Osiejuk
Department of Behavioral Ecology, Institute of Environmental Biology, Faculty of Biology,
Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland

Conventional communication, like human speech or the bee dance, consists of arbitrary signals associated with meaning through convention. Acoustic conventions seem to be frequent among passerine birds having song repertoire variability, but such behaviors are unknown in nonpasserine species producing simple calls. Because the variability of vocalizations is relatively small in nonpasserine birds, no study has investigated their ability to create conventional signals. We experimentally show here that Corncrake males (*Crex crex*), modifying rhythm in simple 2-syllable calls, signal their neighbors about their aggressive motivation. Males responded more aggressively (approached the speaker and attacked it) to playbacks with intermittent than with monotonous rhythm, and males calling with a more intermittent rhythm were more aggressive. The presence of convention in this system requires that the production of alternative signals is not linked with differential production costs. In Corncrakes, aggressiveness is signaled by a signal with lower production cost (lower call rate) than the lack of aggressiveness, and our results indicate that the honesty of the rhythm is maintained by a receiver retaliation cost rather than by production costs. Our observations suggest that temporal organization of signals in Corncrakes is an example of syntax, equivalent to a very simple Morse code system. *Key words:* aggressiveness, call rhythm, *Crex crex*, motivation, syntax. *[Behav Ecol 21:1203–1210 (2010)]*

Conventional signals are the signals with a meaning that is arbitrary with respect to the signal's design and therefore dependent for meaning on an agreement between the signaler and receiver (sense 2 of Guilford and Dawkins 1995). They are honest by definition if the interests of the sender and receiver are identical in an evolutionary sense; however, they are highly vulnerable to deception if the interests of both sides are opposing (Searcy and Nowicki 2005). Therefore, the honesty of conventional signals in agonistic interactions must be connected with some stabilizing cost (Zahavi 1975; Maynard Smith 1994; Zahavi Am and Zahavi As 1997; Vehrencamp 2000; but see Lachmann et al. 2001). Nevertheless, in order to maintain signal arbitrariness, costs should not be paid directly during the production of the signal but they should be receiver dependent (Guilford and Dawkins 1995). Hence, conventional signals have been popularly understood as cost–free signals, whereas they should be rather considered as minimal signals (Maynard Smith and Harper 1995, 2003; Számadó 2003), that is, the signals for which production cost is used only in signal transmission but that is not used to verify signal meaning (Számadó 2003). Models proposed 2 kinds of receiver-dependent costs: receiver retaliation (Enquist 1985) and vulnerability handicap (Zahavi 1987; Adams and Mesterton-Gibbons 1995). Whereas the role of the first one in conventional signaling has been empirically proved (Molles and Vehrencamp 2001), the evidence for the second one is contradictory (Zahavi 1987; Számadó 2003, 2008; Laidre and Vehrencamp 2008; Searcy et al. 2008).

The most expressive examples of conventional communication are the bee dance and human speech; however, there are many others. Typical examples are color plumage badges in birds (Rohwer 1982; Møller 1987; Pärt and Qvarnström

1997; Pryke et al. 2002) signaling the status of the sender. Although they cannot be varied on a short timescale, they are low-cost signals that have evolved to be linked with fighting ability and motivation. Nevertheless, the assertion that badges of status are conventional signals is problematic. Because deception has not been observed in nature (Searcy and Nowicki 2005), they can be so-called indices, the correlates of physical attributes of senders. Other possible examples of visual signals that may be conventional signals include eyespots of Anolis lizards (*Anolis carolinensis*) (Korzan et al. 2000) and the striped barring in Swordtail fish (*Xiphophorus*) (Morris and Casey 1998; Moretz and Morris 2003). Conventional signals may also include olfactory (Poole 1989) and acoustic signals. Acoustic conventional signals, Anolis eyespots, and fish bar marks can be changed on a relatively short timescale, and they differ from plumage badges because they allow for short-term communication. Research to date has shown that song-type matching and switching rate are conventional signals in the Banded Wren (*Thryothorus pleurostictus*) and Song Sparrows (*Melospiza melodia*) (Molles and Vehrencamp 2001; Vehrencamp 2001, 2007). In general, bird songs and calls are highly versatile, and theoretically, such meaningful units can be arranged in a nearly unlimited number of combinations, which creates many possibilities for information coding (Freeberg and Lucas 2002). In particular, the ability to temporally organize songs and calls creates the possibility for a specific conventional system based on the ordered use of appropriate symbols for issuing signals, that is, syntax. This system would be equivalent to a very simple Morse code system.

The Corncrake (*Crex crex*) is a territorial rail inhabiting marshy grasslands. Its call is simple, loud, and can be performed nearly continuously throughout most of the night at a high rate, up to 10 000 calls per night. The Corncrake call is functionally equivalent to songs of passerines with relatively simple repertoires, and its syllables are equivalent to song types in oscines (Cramp and Simmons 1980; Schäffer 1995). The call consists of 2 syllables (the first syllable is slightly shorter than the second one) repeated in long bouts
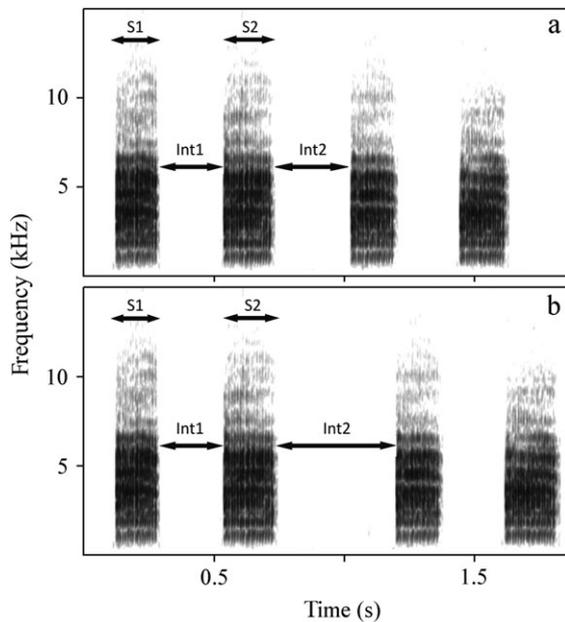
Figure 1
Temporal structure of Corncrake calls. In natural intermittent calls (b), second intervals (Int2) are always longer than first intervals (Int1), whereas in natural monotonous calls (a), they are indistinguishable.

(Figure 1), and the key parameter that seems to encode aggressive information is the interval between subsequent calls (Int2) (Osiejuk et al. 2004). The inner syllable structure is individually distinctive and stable for longer periods (Peake et al. 1998; Peake and McGregor 1999). When the interval between calls (Int2) is similar to the interval between the 2 syllables within a call (Int1), the pattern of calling is very regular and sounds "monotonous." When the interval between calls increases (Int2), the calling sounds "intermittent." We expressed this variability in a simple variable that we called "rhythm" (Figure 1), which was calculated as the ratio of the interval between calls to the total duration of the call (ranging continuously from about 0.4 to about 1.3 [see Materials and methods]). The rhythm of individuals may change during the night (mean standard deviation [SD] of 6 males recorded 3 times during the night = 0.06) and the season (mean SD of 9 males recorded 4–6 times during the season = 0.06) (Osiejuk TS, unpublished data) and is more intermittent during periods of territory establishment (Osiejuk et al. 2004). In addition to seasonal effects, higher values of rhythm are positively correlated with male body size (Osiejuk et al. 2004).

Given this information and preliminary observations, we hypothesize that during interactions, Corncrake males use a conventional signaling strategy (Enquist 1985; Johnstone and Norris 1993; Hurd 1997; Enquist et al. 1998; Hurd and Enquist 1998; Vehrencamp 2000) to indicate aggressive motivation. According to this strategy, during the interaction, a more aggressive male should call with a more intermittent rhythm than a less aggressive male, it should attack a rival signaling a similar aggressiveness (calling with a similar rhythm), flee from a rival signaling a higher aggressiveness (calling with a higher rhythm), and give a chance to flee to a rival signaling lower aggressiveness (calling with a lower rhythm). We tested this ideas in 3 series of experiments with noninteractive playback where we considered receiver as well as sender perspectives (Hurd and Enquist 2001; Vehrencamp et al. 2007). In the first experiment (E1), we used playback recordings with natural intermittent and monotonous calls. We asked whether calls with intermittent versus monotonous

rhythm were more likely to initiate aggressive responses. In the second experiment (E2), we lengthened Int2 of natural monotonous calls and shortened Int2 of natural intermittent calls. We asked whether calls with natural syllables but manipulated rhythm provoked analogous reactions as their natural equivalents. In the third experiment, we used fully synthetic syllables in calls with either intermittent or monotonous rhythm. We asked whether the code contained in call rhythm was functional, even if the call did not comprise any individually specific information. Then, considering the data from all experiments, we analyzed how the aggressive behavior of males was influenced by the rhythm level of territorial males and the difference between their rhythm and the playback. Because inference on the signal function based solely on the signal broadcast on a subject's territory can be inconclusive (Searcy et al. 2006, 2008; Laidre and Vehrencamp 2008; Searcy and Beecher 2009), this analysis is to provide further insight into the signal function and to depict more precisely a male's behaviors in the context of its own vocal signals (Hurd and Enquist 2001; Vehrencamp et al. 2007). We used a compound measure of male reactions (mode of approach—MA), which jointly quantifies directions of movements during the experiment and the distance to the speaker as our index of male aggressiveness (see Materials and methods). The interpretation of MA corresponds approximately to the average angle deviation of the move of a bird from the shortest line between it and the speaker throughout the experiment, and low values of MA represent closer and/or faster approach to the speaker, that is, higher aggressiveness.

MATERIALS AND METHODS

Study area and subjects

The study was carried out in Kampinoski National Park (NP) in Poland ($20°23'$E and $52°19'$N) in the spring of 2007 and 2008. In the study area (ca. 24 km²), Corncrakes were irregularly distributed, and basic parameters of abundance and habitat selection are known from earlier studies (Osiejuk and Olech 2004; Osiejuk et al. 2004). We also present the data from experiments carried out in 2010 in the same localization.

Preparation of call stimuli

For the playback experiments, we used a Philips Magnavox ESP25 (Suzhou, China) compact disc player with a wireless SEKAKU WA-320 (Taichung, ROC Taiwan) loudspeaker with 20 W amplifier and 50–15 000 Hz frequency range. Each experiment used a different set of calls belonging to 1 of 3 kinds of stimuli:

Natural call stimuli
We have a database of >700 recordings belonging to >100 males recorded in the study area between 2001 and 2004. Call rhythm was defined as:

$$\text{Rhythm} = \frac{\text{Interval2}}{\text{Syllable1} + \text{Interval1} + \text{Syllable2}}.$$

Call rhythm was calculated for each recording, and it ranged from 0.427 to 1.271 (Figure 1). Out of these recordings, we selected the 38 samples with the highest rhythm and the 38 samples with the lowest. Then from these samples, we randomly selected 18 intermittent recordings (mean rhythm = 0.999, minimum rhythm = 0.849) and 18 monotonous recordings (mean rhythm = 0.515, maximum rhythm = 0.554;

t-test: $t = 18.01$, $P < 0.001$). Each sample was obtained from a different male and was used only once.

Computer-modified call stimuli

From the sample of the above-mentioned recordings that had not yet been used (40 recordings), we randomly chose 18 intermittent and 18 monotonous ones. In the next step, we removed silence from Int2 of intermittent call samples and added silence into Int2 in all monotonous call samples, keeping other parameters constant. As a result, we obtained a set of originally intermittent calls that sounded like monotonous calls (mean rhythm = 0.601, maximum rhythm = 0.701) and a set of originally monotonous calls that sounded like intermittent calls (mean rhythm = 1.026, minimum rhythm = 0.958; *t*-test: $t = 21.01$, $P < 0.001$).

Modifications were performed in pairs of samples, namely, with a randomly chosen intermittent and monotonous sample. We lengthened Int2 of the monotonous sample so that it reached exactly the same rhythm as the intermittent sample from the pair and vice versa. As a result, the distribution of rhythms in the set was identical before and after modifications.

Synthesized call stimuli

Synthetic calls were produced with Adobe Audition 1.5 in 4 steps, and the target call characteristics were based on call variation in this population (Osiejuk and Olech 2004; Osiejuk et al. 2004). First, a single pulse of 6 ms in duration was generated with Generate Noise (white) function. Second, the pulse was copied and pasted to make a sequence of pulses occurring at a natural rate. Whereas the within-syllable pulse rate was kept at an average level, the pulse-to-pulse durations between successive pulses were alternately longer and shorter than what is typical for natural calls (May 1998; Peake et al. 1998). The first syllable (S1) consisted of 16 pulses (duration 180 ms) and the second syllable (S2) had 18 pulses (duration 199 ms). The first 16 pulses of S2 had the same time distribution as the first 16 pulses of S1. Third, we used an Fast Fourier Transform filter to change the initially flat energy distribution in the frequency domain to an averaged spectrum calculated for 20 randomly selected males from the study area. Thus, synthetic calls had a Corncrake-specific call spectrum but were not biased toward any single individual. Fourth, we copied synthetic calls, that is, sequences of S1 + Int1 + S2 + Int2, in such a way that we obtained 2 types of stimuli, one with a monotonous rhythm and one with an intermittent rhythm. For the monotonous rhythm, we used Int1 = 320 ms and Int2 = 350 ms, which resulted in a rhythm = 0.5. For the intermittent rhythm, we used Int1 = 300 ms and Int2 = 800 ms, which resulted in a rhythm = 1.178. These 2 playback sequences were used in all replicates. All these calls were digitally prepared to match a 96 ± 5 dB signal pressure level (at 1 m) (natural amplitude).

Experiments and treatments

We performed 3 series of experiments with the same design but different treatments (E1—with natural call stimuli; E2—with computer-modified call stimuli; E3—with synthesized call stimuli). Each experiment consisted of 2 treatments (with monotonous or intermittent rhythms) that were conducted in a random order for each subject. Each treatment for an individual male was conducted on different nights within 48 h. Each pair of trials for all 3 series of experiments was conducted on different males ($n = 18$, 18, and 17 males, respectively).

We also present 40 experiments conducted in 2010 in order to examine the actions of senders calling with different

rhythms. In these experiments, focal males were tested only once. Song stimuli were broadcast interactively for 5 min, and the rhythm of the stimuli was standardized to 0.85 (mean rhythm + 1 SD). During the playback, we noted the number of attacks on the speaker as the response variable. In the remaining issues, these experiments were carried out and analyzed identically as the 2007–2008 experiments.

Playback protocol

Experiments were carried out between 17 and 28 May 2007 and 14 May and 9 June 2008 (between 2200 and 0400 h local time).

Before each experiment, the loudspeaker was placed <0.5 m above the ground within the subject male's territory. All the experiments were conducted within an acoustic location system, which consisted of an array of 4 omnidirectional microphones (Sennheiser K6/ME 62) recording to an Edirol R-4 Pro 4-channel Portable Recorder and Wave Editor (Hamamatsu, Japan). Microphones were fixed at 2.5 m above the ground. 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.

Each experiment lasted 7 min and consisted of the following stages: 1) 1 min of silence (PREPLAY), followed by 2) eight 20-s playbacks separated by seven 20-s silence intervals (PLAY), and then 3) 1 min of silence (POST). We started the second stage only if we recorded calling during the PREPLAY stage.

Calls during the PLAY stage consisted of an alternating playback with 20-s gaps for 2 reasons: first, we observed during trial experiments that focal males frequently called and calmed down alternately, most probably localizing the position of the calling intruder, and second we wanted to avoid strong overlap of calls (male and playback) on whole recordings.

Data analysis

Reactions of males to playbacks during experiments are complex, and no single variable can describe them comprehensively. 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 intentions, but separately they only partially convey the picture of responses. For example, during the experiment, a male might have approached the speaker a few times and flown away without a definitive attack. Therefore, we created a more complex measure that has the virtues of the above variables and minimizes their flaws. We called it MA because it provided a comprehensive measure of a male's behavior throughout the experiments, and it was strongly linked with the probability of attack on the speaker (Wald $\chi^2 = 8.22$, $P = 0.004$). MA is given by the formula:

$$\text{MA} = \frac{1}{9} \sum_{s=0}^{8} \left[\arccos\left(\frac{d_b - d_a}{d_r} \right) \times \log_9 d_a \right],$$

where s = time section (0 = during PREPLAY; 1–8 = during PLAY and POST), d_b = distance to the speaker before the section, d_a = distance to the speaker after the section, and d_r = the real distance covered. A MA 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.

This measure includes a correction for distance ($\log_9 d_a$) that is important because of some restrictions to motion

Table 1

Factors associated with the intensity of male responses

	MA			Number of attacks		
	Wald χ^2	df	P	Wald χ^2	df	P
Intercept	0.60	1	0.440	3.42	1	0.064
Playback	17.25	1	<0.001	10.74	1	0.001
Playback × rhythm	14.39	2	0.001	10.99	2	0.004
Playback × difference	22.76	2	<0.001	10.05	2	0.007
QIC/QICC	50.41/52.74			82.70/88.50		

Generalized estimating equations model including playback treatments (I, M), rhythm (rhythm before experiment), and difference (between rhythms of the male and playback). Wald statistics and P values express summary contribution of each factor to the variance of the response variable. QIC, quasi-likelihood under independence model criterion; QICC, QIC corrected version.

during experiments. 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 outwards decreased much more than the MA of a bird that was closer and moved outwards. Conversely, if a bird was close to the speaker and moved some distance inwards, its MA increased more than that of a bird moving the same distance inwards but from a further position. The base of the logarithm (here we used 9) determines the critical distance below and above which the MA of males started to increase and decrease, respectively. We chose this value because it minimizes the skewness of the MA distribution, and thus, it provides the best ratio of penalties to rewards. Therefore, it seems that crossing this distance inwards or outwards from the speaker is by itself an indicator of aggressive or submissive behavior, and this generally agrees with our field observations (see also Számadó 2008).

Given that MA implies a nontrivial transformation of the original data, we include the results of a more traditional analysis with the number of attacks as response variable to assess the suitability of this measure and to prove that the current patterns are not artificially generated by the index we use (Tables 1 and 2).

Statistical analysis

We used generalized estimating equations (SPSS 16.0 software) to analyze paired experiments with playback. The models and parameters were selected using the quasi-likelihood under independence model criterion (for choosing the best correlation structures) and its corrected version (for choosing the best subsets of predictors). Models with different response variables (MA and the number of attacks on the speaker) were fitted independently. To fit models, we used the approach advocated by Burnham and Anderson (2002). In particular, we did not mix null hypothesis testing with information-theoretic criteria. During the model-fitting process, we used the following categorical variables and covariates: experiments (E1–3), playback treatments (I, M), rhythm (rhythm of the male before experiment), difference (between rhythms of the male and playback), absolute difference, distance (distance to the speaker of the male at the beginning of the experiment), hour, date, year, and sequence of playbacks (I first vs. M first). In order to fit 2 final models (one for each response variable), we compared several dozen of initial models with all possible combinations of factors and covariates up to third degree factorial.
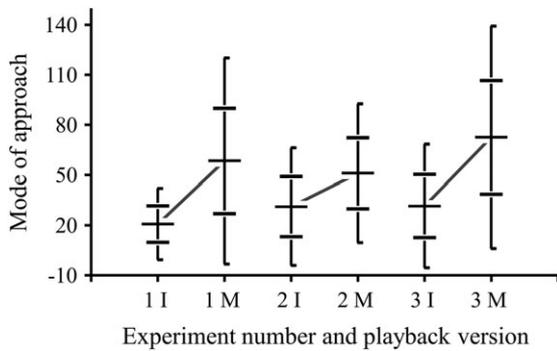
Because the values of MA can be interpreted as waiting times, in models with MA as the dependent variable, we fitted the data using a gamma distribution. In models with the number of attacks on the speaker as the dependent variable, we fitted the data using a negative binomial distribution. This distribution is especially useful for discrete data over an unbounded positive range whose sample variance (=15.69) exceeds the sample mean (=1.67) (McCullagh and Nelder 1989). In all analyses, the data were controlled for repeated measurements (monotonous vs. intermittent playback), and in case of t-tests, the data were controlled for normality (Shapiro–Wilk test). All P values are 2 tailed.

RESULTS

Rhythm and motivation—receiver behavior

We used noninteractive playbacks to test whether the responses of males ($n = 53$) differ relative to playbacks with either intermittent or monotonous rhythm. We found evidence that responses of males (MA and the number of attacks) differed with respect to playbacks with intermittent calls and monotonous ones (Tables 1 and 2, Figure 2). The difference was independent of playback modification (Figure 2).

To rule out any effects of body size or individual male identity on responses, in experiment 3, we used playbacks

Table 2

Estimates of parameters associated with the intensity of male responses

	MA				Number of attacks			
	Estimate	Standard error	Wald χ^2	$P_{(df = 1)}$	Estimate	Standard error	Wald χ^2	$P_{(df = 1)}$
Intercept	169.53	48.03	12.46	<0.001	−0.83	0.23	12.96	<0.001
Playback-I	−288.10	69.36	17.25	<0.001	1.18	0.36	10.74	0.001
Playback-M	0[a]				0[a]			
Playback-I × rhythm	173.96	53.60	10.53	0.001	−0.41	0.25	2.85	0.092
Playback-M × rhythm	−168.78	82.81	4.15	0.042	1.09	0.33	10.58	0.001
Playback-I × difference	−196.81	45.50	18.71	<0.001	0.57	0.24	5.51	0.019
Playback-M × difference	132.52	70.10	3.57	0.059	−0.79	0.30	6.94	0.008

Estimates of generalized estimating equations model including 2 playback treatments, rhythm (before experiment), and difference (between rhythms of the male and playback) as effects.

[a] Baseline categories of the categorical variable. P values pertain to the significance of estimates (slopes of covariates or differences between subsets of categorical variables).
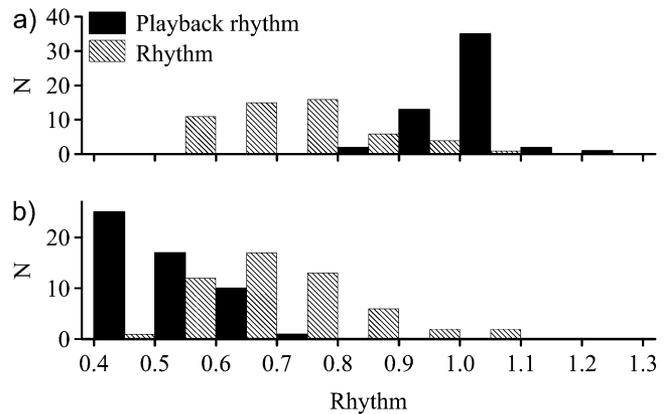
Figure 2
Differences between male responses (MA) in 3 experiments with 2 playback versions. I, intermittent playbacks and M, monotonous playbacks. 1, E1; 2, E2; and 3, E3. Thick horizontal lines are marginal means, midsize horizontal lines are ±standard error, vertical lines are ±95% confidence intervals. Low values of MA represent closer and/ or faster approach to the speaker. The data come from a model with 2 additional effects (experiments E1–3, interaction between experiment and playback treatments) compared with the model from Table 2.

Figure 3
The distributions of call rhythm of focal males (Rhythm) and playbacks (Playback rhythm) in experiments with intermittent playbacks (a) and monotonous playbacks (b).

consisting of artificial syllables (see Materials and methods). Males responded differently to intermittent and monotonous playback in E3 and similarly as in E1 and E2 (Figure 2), indicating that intra-syllabic variability is not necessary for signaling motivation but that rhythm alone can clearly signal motivation in the Corncrake.

Rhythm and motivation—sender behavior

We examined the degree to which male aggressiveness (MA and the number of attacks) was correlated with its rhythm from before the experiment and the difference between its rhythm and the rhythm of the playback (male's rhythm minus playback rhythm).

In the studied population, only a small fraction of males called with a higher rhythm than the rhythm of a playback when the playback was intermittent (Figure 3a) and a majority of males called with a higher rhythm than the rhythm of a playback when the playback was monotonous (Figure 3b). Consequently, the differences of the rhythm of the male and playback were significantly smaller during experiments with intermittent playbacks than during experiments with monotonous ones (intermittent difference: mean, range = −0.34, −0.65 to 0.02; monotonous difference: mean, range = 0.17, −0.12 to 0.53; t-test for dependent samples: $t = −27.17$, degrees of freedom (df) = 52, $P < 0.0001$). During experiments with monotonous playbacks (range of playback rhythms: 0.427–0.701), males that were calling with a higher rhythm prior to experiment and with a lower rhythm difference responded more aggressively to playbacks (had lower MAs and attacked the speaker more frequently) (Table 2). It means that the most aggressive were interactions when males were calling with a rhythm similar to the playback and when the rhythm of males was in the upper part of the range of the playback rhythms (Figure 3b). Aggressive responses were unlikely when males were calling with a much higher or much lower rhythm than the playback. During experiments with intermittent playbacks (range of playback rhythms: 0.849–1.271), males that were calling with a lower rhythm prior to experiment and with a higher rhythm difference responded more aggressively to playbacks (Table 2). Considering the distributions of rhythms of territorial males and intermittent

playbacks (Figure 3a) and the fact that the highest rhythm difference barely exceeded 0, this result did not differ from the one that we received for monotonous playbacks. The intensity of responses was negatively correlated with the rhythm of males because only males that were calling with rhythms in the lower part of the range of intermittent playbacks had similar rhythms to playbacks. By contrast, most of intermittent playbacks might be perceived as too intimidating for approach (see de Kort et al. 2009).

To show that this interpretation is correct and that intermittent rhythm is a signal that predicts aggression, we tested males with playbacks (each one coming from a different male) with the same rhythm (rhythm = 0.85). These results were derived from 2010 playback trials, on a sample of 40 males. The number of attacks was positively correlated with the rhythm of focal birds (negative binomial regression: estimate ± standard error = 8.49 ± 2.64; Wald $\chi^2 = 10.32$, df = 1, $P = 0.001$). Consequently, we conclude that the reactions of males during experiments with intermittent and monotonous playbacks were consistent with a conventional signaling strategy (see in the Introduction). We also conclude that calling rhythm meets the criteria to establish it as an aggressive behavior (Searcy and Beecher 2009) and that intermittent and monotonous rhythms code for high and low aggressive motivation, respectively.

DISCUSSION

During agonistic interactions, a signal must meet 2 requirements in order to be considered conventional. The signal should be subject to a receiver retaliation rule instead of being stabilized by production or vulnerability costs, and its form should be arbitrary (Enquist 1985; Guilford and Dawkins 1995; Vehrencamp 2000).

Considering only receiver-independent costs, conventional signals, by definition, have only an efficacy cost, which means they are minimal signals (Maynard Smith and Harper 1995, 2003; Számadó 2003). Thus, the difference between costs of alternative signals should not exceed the difference between their efficacy costs (Hurd and Enquist 2005). Consequently, as long as the signal production cost does not exceed the cost necessary to transmit the information unambiguously and the difference between alternative signals is not sufficient to handicap the individual producing the more costly signal, we can assume that the signal meets one of the requirements of conventionality. Because the transition from intermittent to

monotonous rhythm of Corncrake calling involves an increase in calling rate, calling with monotonous rhythm takes more energy. Such increase of production costs is common among amphibians (Ryan 1988), though it concerns also song rate in some passerine birds (Eberhardt 1994). Vehrencamp (2000) suggested, however, that if song rate was used in a gradual scale associated with aggressive motivation, then it is more likely that the system would be stabilized by the subsequent fight than by the higher production cost. Moreover, Számadó (2003) demonstrated that minimal signals are evolutionarily stable strategy against handicap signals even if cheating is common, whereas handicap signals are not evolutionarily stable against the invasion of minimal signals. Therefore, from the evolutionary point of view, it is more likely that if a change of song/call rate transmits on average a sufficient amount of information and if such change is not associated with a considerable change in the production cost, then individuals should rather ignore this cost and inspect each other. For example, in domestic roosters, the production cost of crowing is marginal (Chappell et al. 1995; Horn et al. 1995), whereas its frequency is significantly linked with the status and aggressiveness of the male (Leonard and Horn 1995). The issue of production costs of song/call rate is strictly connected with who is the signal receiver. Collins (2004) suggested that song rate is more frequently a signal directed at females than at rivals. Vehrencamp (2000) in turn indicated that song rate can function concurrently as a handicap signal for females and as a conventional signal for males. Hence, it is intriguing whether short-term changes in the pace of singing in many songbirds should be classified as handicaps or whether they should be regarded as conventional signals. Because during reproductive seasons males sing intensively to attract females, the benefits of linking 2 messages in one signal would be 3-fold: the lack of production cost (or very small cost) of sending a message to the rival because the cost would be paid anyhow, no fitness cost in terms of attracting fewer females when signaling only for males, and no need to develop 2 independent signals. All acoustic conventional signals used during male–male interactions that have been described so far are at the same time signals for females (Vehrencamp 2000, 2001).

The fact that Corncrakes call very intensively implies that in the longer timescale, males may pay high signal production costs. Nevertheless, regarding signal intensity, Corncrake calls are largely directed toward females because paired males either markedly decrease the intensity of calling or cease calling (Tyler and Green 1996). Considering the fact that the signal of smaller intensity is the aggressive one and vice versa, it can be concluded that this system is not stabilized by production costs. Furthermore, males also do not pay a vulnerability cost because the distance between simultaneously calling males is seldom smaller than 50 m and the habitat of Corncrakes (and the darkness) practically prevents males from seeing one another until they are very close. Finally, the rhythm is not an index of a male because males can freely change it, either during the night or during the season (see in the Introduction). Taking into consideration the above discussion and results, we conclude that the only cost paid by Corncrake males calling with intermittent rhythm to the rival is possible retaliation. The results from both the receiver and the sender perspectives show together that the level of rhythm signals aggressive motivation. Males were more likely to approach and to attack the speaker when the playback was intermittent and when their rhythm was similar to the rhythm of the playback. In addition, males sending calls with higher rhythm were more aggressive.

The second requirement of conventionality of the signal is its arbitrariness. The best evidence for arbitrariness is to show that the signal's meaning can work in opposite ways in different species, as Vehrencamp (2000) showed for song-type switching rates in songbirds. Nevertheless, it does not pertain to all signal types because, for example, song-type matching meets this requirement only at the level of an individual (Vehrencamp 2001). Considering only the production cost of aggressive (intermittent) versus nonaggressive (monotonous) calls of the Corncrake, the opposite coding takes place in rosters (Leonard and Horn 1995), where more aggressive males crow more frequently. Nevertheless, the comparison of the rhythm with call rate is a large simplification. The transition from monotonous to intermittent rhythm is not restricted only to a decrease in call rate, but it is an unambiguous transformation of the arrangement of syllables (Figure 1). Thus, it is an example of syntax. The rhythm of the Corncrake calls is very specific; both aggressive and nonaggressive signals use the same vocalizations and hence the same vocal structures. The monotonous signal is the simplest possible one made of one vocalization (even pauses and the lack of discernible pairs or orders of syllables), and analogous signals are widespread in many species (Gerhardt et al. 2007). By contrast, the intermittent signal is characterized by a more intricate arrangement of syllables, and it expresses a more complex information. The monotonous call is therefore the most likely default signal, analogous to the lack of song-type matching in some passerine birds (Vehrencamp 2000), and the intermittent call should be treated as one of the theoretically infinite number of syntactic combinations of one vocalization. Hence, to demonstrate the arbitrariness of call rhythm in the Corncrake, we should not look for a set of signals with the opposite meaning. We should rather look for a system in which a nonaggressive (default—the lack of interest in competition, passivity) signal would make the simplest combination of vocalizations (either monotonously repeated single element as in the Corncrake call or the simplest or random combination of a few elements in complex signals), whereas an aggressive signal would be coded in a more or less intricate temporal combination of basic elements. For example, Carolina chickadees (*Poecile carolinensis*) respond differently to A, B, C, and D notes composition and ordering within a call (Freeberg and Lucas 2002; Clucas et al. 2004; Mahurin and Freeberg 2008). Some combination (e.g., the ratio of D notes to other note types) may function as aggressive signals; however, among Chickadee species, the contextual differences of note use vary markedly (Freeberg and Lucas 2002). Analogous systems of information coding can be found in many groups of animals (for review, see Crockford and Boesch 2005), though the knowledge of their meaning and context comes from correlations. All these studies show clearly, however, that signals based on syntax are stable combinations of basic elements and that the number of possible arrangement conveying a single message in different species is infinite. Because there is no reason to suspect that intermittent rhythm of the Corncrake call is in any way constrained (males sometimes make mistakes creating different combinations of syllables), we conclude that the call rhythm of the Corncrake meets the requirement of arbitrariness.

Given that the ratio of syllable length to silence of the aggressive signal is lower than the submissive one, why is the intermittent rhythm the more aggressive signal and the monotonous rhythm the less aggressive? This phenomenon can be interpreted by 2 complementary explanations. Hurd (1997) created a model that showed that stronger individuals have less to gain by avoiding escalated contests and are thus more sensitive to signal costs. As a result, higher costs of signal production in weaker males are balanced by a lower probability of retaliation and vice versa, and the costs paid in resolving contests are highest for closely matched opponents. Alternatively, calling with the regular monotonous pattern could mean

that a male is advertising for females or territory ownership without wanting to interact aggressively (leaving no silent gaps and ignoring any replies), whereas the intermittent pattern means the male is leaving a silent gap to listen for replies from other males and trying to keep them at bay. In other words, if there are no females in the vicinity, it may be advantageous for a male to call monotonously (higher probability of being heard), to be interested only in females' attraction, and to ignore other males, but when females arrive at the territory, then a male could be more interested in keeping other males at bay and less in female attraction. The first explanation is supported by the result that conflicts between males were contingent on the difference between their rhythms. The second explanation is supported by the fact that males call rarely or not at all when paired (Tyler and Green 1996), and it agrees with the fact that the Corncrake call can function simultaneously as a signal for males and females. We claim, however, that listening to rivals does not put a biological constraint on the arbitrariness of the intermittent rhythm. When disturbed, Corncrakes create calls with long pauses (instead of Int1 and Int2) and low syllable rate that sound monotonous or disconnected. In contrast, a change from monotonous to intermittent rhythm is limited only to lengthening of the second interval, keeping the first one constant. It means that even if intermittent rhythm can be helpful in listening to rivals, it has not evolved in order to do that.

This paper relies partially on statistical tests performed on a new measure of response to playback (MA), and therefore, we provided the information required to assess the suitability of this measure (Tables 1 and 2). The use of a microphone array for objective measurement of subjects' positions and movements represents an important improvement over the more typical visual estimates. The data collected in this way are multidimensional, and it is difficult to explore them in a single analysis. In contrast, the number of attacks is a very clear and straightforward measurement of aggressiveness of an individual, but fights are rare and using them as the response variable compels scientists to collect large samples. Because of this and a striking similarity between the results based on MA and the number of attacks, we think that the use of a single but multidimensional summary measurement of subject responses seems superior to the multiple separate but correlated response measurements that are analyzed in many playback experiments. Moreover, our measurement seems to have some advantages over more traditional methods of variable reduction (e.g., principal components analysis).

In conclusion, our data on interactions between Corncrake males indicate that signals coded in the rhythm of calling have conventional character. This example shows that even very simple rules, like the variability of the temporal arrangement of elements within a vocalization, can be a conventional signal. This code represents a very refined yet simple example of syntax. Because equivalent temporal variability of vocalizations is present in some form in many taxa, similar signals may be widespread.

REFERENCES

Adams ES, Mesterton-Gibbons M. 1995. The cost of threat displays and the stability of deceptive communication. J Theor Biol. 175:405–421.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference. A practical information-theoretic approach. New York: Springer.

Chappell MA, Zuk M, Kwan TH, Johnsen TS. 1995. Energy cost of an avian vocal display: crowing in red junglefowl. Anim Behav. 49:255–257.

Clucas BA, Freeberg TM, Lucas JR. 2004. Chick-a-dee call syntax, social context, and season affect vocal responses of Carolina chickadees (Poecile carolinensis). Behav Ecol Sociobiol. 57:187–196.

Collins S. 2004. Vocal fighting and flirting: the functions of birdsong. In: Marler P, Slabbekoorn H, editors. Nature's music: the science of birdsong. London: Elsevier Academic Press. p. 39–79.

Cramp S, Simmons KEL. 1980. The birds of the Western Palaearctic. Vol. 2. Oxford: Oxford University Press.

Crockford C, Boesch C. 2005. Call combinations in wild chimpanzees. Behaviour. 142:397–421.

de Kort SR, Eldermire ERB, Cramer ERA, Vehrencamp SL. 2009. The deterrent effect of bird song in territory defense. Behav Ecol. 20:200–206.

Eberhardt LS. 1994. Oxygen consumption during singing by male Carolina wrens (Thryothorus ludovicianus). Auk. 111:124–130.

Enquist M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. Anim Behav. 33:1152–1161.

Enquist M, Ghirlanda S, Hurd PL. 1998. Discrete conventional signalling of continuously varying resource value. Anim Behav. 56:749–753.

Freeberg TM, Lucas JR. 2002. Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees, Poecile carolinensis. Anim Behav. 63:837–845.

Gerhardt HC, Humfeld SC, Marshall VT. 2007. Temporal order and the evolution of complex acoustic signals. Proc R Soc Lond B Biol Sci. 274:1789–1794.

Guilford T, Dawkins MS. 1995. What are conventional signals? Anim Behav. 49:1689–1695.

Horn AG, Leonard ML, Weary DM. 1995. Oxygen consumption during crowing by roosters: talk is cheap. Anim Behav. 50:1171–1175.

Hurd PL. 1997. Is signaling of fighting ability costlier for weaker individuals? J Theor Biol. 184:83–88.

Hurd PL, Enquist M. 1998. Conventional signalling in aggressive interactions: the importance of temporal structure. J Theor Biol. 192:197–211.

Hurd PL, Enquist M. 2001. Threat displays in birds. Can J Zool. 79:931–942.

Hurd PL, Enquist M. 2005. A strategic taxonomy of biological communication. Anim Behav. 70:1155–1170.

Johnstone RA, Norris K. 1993. Badges of status and the cost of aggression. Behav Ecol Sociobiol. 32:127–134.

Korzan WJ, Summers TR, Ronan PJ, Summers CH. 2000. Visible sympathetic activity as a social signal in Anolis carolinensis: changes in aggression and plasma catecholamines. Horm Behav. 38:193–199.

Lachmann M, Számadó S, Bergstrom CT. 2001. Cost and conflict in animal signals and human language. Proc Natl Acad Sci U S A. 98:13189–13194.

Laidre ME, Vehrencamp SL. 2008. Is bird song a reliable signal of aggressive intent? Behav Ecol Sociobiol. 62:1207–1211.

Leonard ML, Horn AG. 1995. Crowing in relation to status in roosters. Anim Behav. 49:1283–1290.

Mahurin EJ, Freeberg TM. 2008. Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. Behav Ecol. 20:111–116.

May L. 1998. Individually distinctive corncrake Crex crex calls: a further study. Bioacoustics. 9:135–148.

Maynard Smith J. 1994. Must reliable signals be costly? Anim Behav. 47:1115–1120.

Maynard Smith J, Harper DGC. 1995. Animal signals: models and terminology. J Theor Biol. 177:305–311.

Maynard Smith J, Harper DGC. 2003. Animal signals. Oxford: Oxford University Press.

McCullagh P, Nelder JA. 1989. Generalized linear models. 2nd Ed. London: Chapman & Hall.

Møller AP. 1987. Social control of deception among status signaling house sparrows *Passer domesticus*. Behav Ecol Sociobiol. 20:307–311.

Molles LE, Vehrencamp SL. 2001. Songbird cheaters pay a retaliation cost: evidence for auditory conventional signals. Proc R Soc Lond B Biol Sci. 268:2013–2019.

Moretz JA, Morris MA. 2003. Evolutionary labile responses to a signal of aggressive intent. Proc R Soc Lond B Biol Sci. 270:2271–2277.

Morris MA, Casey K. 1998. Female swordtail fish prefer symmetrical sexual signal. Anim Behav. 55:33–39.

Osiejuk TS, Olech B. 2004. Amplitude spectra of Corncrake calls: what do they signalise? Anim Biol. 54:207–220.

Osiejuk TS, Olech B, Ratynska K, Owsinski A, Gromadzka-Ostrowska J. 2004. Effects of season, plasma testosterone and body size on corncrake (*Crex crex*) call rhythm. Ann Zool Fennici. 41:647–659.

Pǎrt T, Qvarnström A. 1997. Forehead patch size predict the outcome of male competition over territories in the collared flycatchers. Anim Behav. 54:893–899.

Peake TM, McGregor PK, Smith KW, Tyler G, Gilbert G, Green RE. 1998. Individuality in Corncrake *Crex crex* vocalizations. Ibis. 140: 120–127.

Peake TM, McGregor PK. 1999. Geographical variation in the vocalisation of the corncrake *Crex crex*. Ethol Ecol Evol. 11:123–137.

Poole J. 1989. Announcing intent: the aggressive state of musth in African elephants. Anim Behav. 37:140–152.

Pryke SR, Andersson S, Lawes MJ, Piper SE. 2002. Carotenoid status signaling in captive and wild red-collared widowbirds: independent effects of badge size and color. Behav Ecol. 13:622–631.

Rohwer SA. 1982. The evolution of reliable and unreliable badges of fighting ability. Am Zool. 33:1325–1331.

Ryan MJ. 1988. Energy, calling and selection. Am Zool. 28:885–898.

Schäffer N. 1995. Rufenhalten und Funktion des Rufens beim Wachtelkönig *Crex crex*. Vogelwelt. 116:141–151.

Searcy WA, Anderson RC, Nowicki S. 2006. Bird song as a signal of aggressive intent. Behav Ecol Sociobiol. 60:234–241.

Searcy WA, Anderson RC, Nowicki S. 2008. Is bird song a reliable signal of aggressive intent? A reply. Behav Ecol Sociobiol. 62: 1213–1216.

Searcy WA, Beecher MD. 2009. Song as an aggressive signal in songbirds. Anim Behav. 78:1281–1292.

Searcy WA, Nowicki S. 2005. The evolution of animal communication: reliability and deception in signaling systems. Princeton (NJ): Princeton University Press.

Számadó S. 2003. Threat displays are not handicaps. J Theor Biol. 221: 327–348.

Számadó S. 2008. How threat displays work: species-specific fighting techniques, weaponry and proximity risk. Anim Behav. 76: 1455–1463.

Tyler GA, Green RE. 1996. The incidence of nocturnal song by male Corncrake *Crex crex* is reduced during pairing. Bird Study. 43: 214–219.

Vehrencamp SL. 2000. Handicap, index, and conventional signal elements of bird song. In: Espmark Y, Amundsen T, Rosenqvist G, editors. Animal signals: signaling and signal design in animal communication. Trondheim (Norway): Tapir Academic Press. p. 277–300.

Vehrencamp SL. 2001. Is song-type matching a conventional signal of aggressive intentions? Proc R Soc Lond B Biol Sci. 268:1637–1642.

Vehrencamp SL, Hall ML, Bohman ER, Depeine CD, Dalziell AH. 2007. Song matching, overlapping, and switching in the banded wren: the sender's perspective. Behav Ecol. 18:849–859.

Zahavi A. 1975. Mate selection—a selection for a handicap. J Theor Biol. 53:205–214.

Zahavi A. 1987. The theory of signal selection and some of its implications. In: Delfino VP, editor. International Symposium of Biological Evolution. Bari (Italy): Adriatic Editrice. p. 305–327.

Zahavi A, Zahavi A. 1997. The handicap principle. Oxford: Oxford University Press.