



## Corncrake males learn new signal meanings during aggressive interactions



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For many animals, the repertoires of songs or calls are relatively small and static during a lifetime. One reason for this is that there are different physiological limitations in the respiratory, phonatory and filter systems in different phylogenetic groups. Nevertheless, learning does not have to be associated exclusively with the acquisition of new vocalizations; individuals may recombine a limited number of elements already present in an individual's repertoire into new sequences. I tested the possibility of learning timing of calls in the corncrake, *Crex crex*, a nonpasserine bird with an extremely low repertoire of calls, using temporal patterns of calls during territorial interactions. I tested whether male are able to comprehend and use a new pattern by connecting known syntax with a new meaning through experience. Experiments with playback demonstrated that males were able to comprehend a new association between the temporal pattern and approaching behaviour of the intruder only after a few minutes of exposure to new circumstances. Additionally, apart from comprehending, males acquired a new signalling strategy; they began signalling their aggressive motivation using the new association. Because comprehension and usage of associations between the syntax of vocalizations and the approaching behaviour of males were modifiable as a result of experience, these results indicate that corncrakes' innate call structures and lack of complex and variable songs allow them to learn the temporal distribution of their calls. This suggests a much broader application and a vital role of contextual learning for the evolution of simple acoustic signalling systems.

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Communication systems of most of the vocally active animals rely on innately programmed sounds and use specific sound types in a limited range of circumstances (Hultsch & Todt 2004; Saranathan et al. 2007; Seyfarth & Cheney 2010). Learning can pertain to the usage and comprehension of known sounds, or contextual learning, as well as the acquisition of new sounds, or vocal learning (Janik & Slater 1997, 2000). The ability to learn contextually appears to be more widespread than vocal learning, because contextual learning requires less elaborate muscle activity of the vocal apparatus (Adret 1992; Janik & Slater 1997). Nevertheless, the ability to mimic vocalizations without comprehension, which exists in many animal groups, indicates that vocal learning does not necessarily imply higher cognitive abilities than contextual learning. The simple mimicry of a sound is a different process from the acquisition of vocalizations that have communicative content (Pepperberg 2002). Although vocal learning must have played a crucial role in the evolution of complex communication

systems, little is known about the role of contextual learning in the evolution of simple acoustic signalling systems, even if the list of animals in which the utterance of a vocalization has been brought under conditional control is vast.

Because of cultural transmission, repertoires of vocalizations used by vocal learning species are generally much larger than those of nonlearning species. However, this is not a rule and there are, for example, nonlearning galliforms with rich and varied repertoires (e.g. red junglefowl, *Gallus gallus*; Collias 1987) and learning passerines with small repertoires (e.g. chaffinch, *Fringilla coelebs*; Slater 1981). There are also animals with very small repertoires of innately programmed calls, for whom vocal communication learning and cultural transmission appear to have no application (e.g. common cuckoo, *Cuculus canorus*). Nevertheless, experience does not have to be associated only with the acquisition of new vocalizations but can also concern the sequencing of different units within a song, i.e. syntax (Hultsch 1991; Hultsch & Todt 1989; Podos et al. 1999; Rose et al. 2004). Here, learning might involve a recombination of subunits of a call or calls already present in an individual's repertoire, which are produced in a new context. Except for the studies on the structure of human language, experiments demonstrating complex rule learning and testing the

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meaning of different syntactic patterns in animals are rather limited (Kershenbaum et al. 2012; ten Cate & Okanoya 2012).

A potential model for studying these issues is specific temporal patterns of calls in rails (Rallidae). Like most of the nonpasserine birds, rails have relatively small repertoires of innate calls; however, some of these vocalizations are produced in a very long series with a specific temporal and structural organization. Both within and between species, such systems can vary in the number of call types (usually one or two), the length of vocalizations (e.g. short and long versions of a single call type) and the length of intervals. Consequently, such repetitive calling can create many possibilities for information encoding (Yip 2006; Hailman 2008). It was shown that the temporal pattern of calls (so-called 'rhythm') in the corncrake, *Crex crex*, is a signalling system based on syntax (Ręk & Osiejuk 2010). In this system, information about a male's aggressive motivation is encoded in sequences of similar vocalizations separated alternately by two intervals (I1 and I2). When subsequent intervals have similar lengths the calling sounds monotonous; when short intervals (I1) alternate with long intervals (I2) the calling sounds intermittent. Because there is no clear dichotomy but a continuous variation, rhythm constitutes a graded signal of aggressive motivation, with syllables given at less regular intervals (more intermittently) by males behaving more aggressively (Fig. 1; Ręk & Osiejuk 2010). Therefore, gradual changes in rhythm have no clear functional explanation, but rather they represent a correlation with motivation. Nevertheless, over the scale of a particular interaction, males compare their rhythm with the competitor's rhythm rather than respond to the absolute rhythm (Ręk & Osiejuk 2010), which means that over a short scale rhythms transmit clear discrete messages. More recently, it was shown that information regarding aggressive motivation in the corncrake is encoded in the syntax itself without being associated with the structure of calls and the absolute length of intervals, which suggests that the design of these patterns is arbitrarily related to their function (Ręk & Osiejuk 2013). This finding implies a more flexible and complex communication system in species with small and innate repertoires, which suggests that there is a possibility for rails, which have innate call structures, to learn timing. Although corncrakes' loud calls very likely play some role in both male–male and male–female interactions, it is unknown whether

the rhythm of calls itself functions in anything except for resolution of territorial conflicts among males. Because a male signalling its motivational state indicates indirectly its potential aggressiveness (Ręk & Osiejuk 2010), rhythm may function both as an announcement between conflicts and as a reliable predictor of the sender's aggressive behaviour before a fight, in a similar way to songs in songbirds.

The aim of this study was to test experimentally whether corncrake males are able to culturally acquire a new syntactic code through the mapping of known syntax with a new meaning. I hypothesize that the arbitrary system of the corncrake is a cultural convention, in which the association between different temporal patterns and their meaning arises as a result of the learning process. With respect to this system, the learning process would require the comprehension of a new signal, which would involve the acquisition of new temporal patterns, or the exchange of already known patterns and mapping between the patterns and their new meaning, and the use of a new signal. This means that a sender should reproduce a signal with a new meaning (Janik & Slater 2000). I tested these ideas in two separate playback experiments that simulated territorial intrusions and examined both comprehension and usage of a new syntactic code.

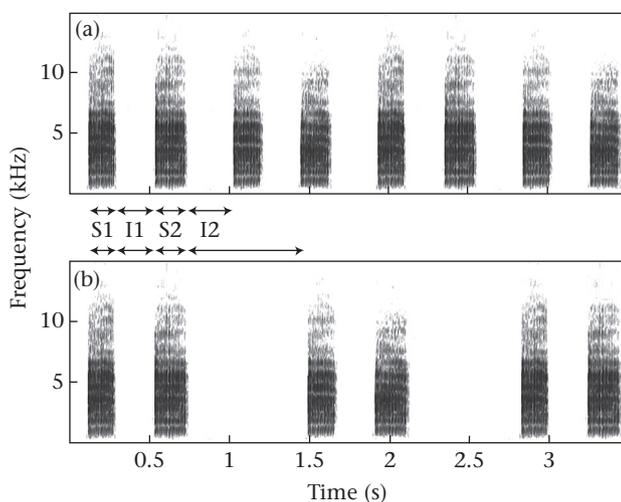
The experiments were based on the observation that the escalation of a territorial conflict by males (decrease of distance) is associated with a gradual change towards a more aggressive-intermittent rhythm, whereas a retreat corresponds with a gradual change towards a more submissive-monotonous rhythm (see below for the data on the natural signalling strategy of males). Therefore, if the researcher simulates an intruder call with a more monotonous rhythm (submissive/de-escalating signal) while approaching the focal male (aggressive/escalating behaviour), such signalling would provide contradictory information to the focal male. Consequently, if rhythm is innately programmed, a male trained to recognize this pattern should still attack mostly intermittently calling intruders during consecutive interactions. If, however, rhythm has a cultural basis, trained males could associate the behaviour of the intruder with a new signal or an old signal with a new behaviour and eventually communicate their motivation using a new signal.

In the first experiment (E1), birds were subjected to the above-mentioned training session before trials. In contrast to the training sessions, which included both approaching and signalling, the experiment included only playback with either a monotonous or an intermittent rhythm, to separate the responses of focal males to signals from responses to escalating behaviour. I asked whether receivers are able to associate the behaviour of the sender with a different syntactic pattern (comprehend). If receivers understood a new signal, they should respond more aggressively to a monotonous pattern than to an intermittent one. Conversely, if the message was misunderstood, subjects should keep responding in the natural way, that is more aggressively to the intermittent pattern. In the second experiment (E2), after the training session, experimental birds received natural playbacks. The objective was to analyse the signalling strategy of the experimental senders and to compare it with the natural signalling strategy of the nonmanipulated senders. If the experimental senders acquired a new (trained) signalling strategy, they should behave differently from nonmanipulated males. In comparison to the nonmanipulated males, the experimental males should call with a more monotonous rhythm while the conflict escalates.

## METHODS

### Study Site and Species

Playback experiments were conducted in the Upper Nurzec River Valley in Northeast Poland (centre of the study area: 23°14'E



**Figure 1.** Sonograms of corncrake calls: (a) broadcast call with a monotonous rhythm; (b) broadcast call with an intermittent rhythm. The rhythm of the broadcast calls was defined as the ratio of the length of the second interval (I2) to the sum of the lengths of the first syllable (S1), first interval (I1) and second syllable (S2). One broadcast call contains a single sequence of S1, I1, S2 and I2. Note that rhythm is not a discrete signal but a graded signal. Sonogram settings: FFT = 1024; frame size = 50%; Hamming window, bandwidth = 122 Hz.

and 52°36'N; ca. 40 km<sup>2</sup>) between 21 May 2012 (sunset/sunrise: 1927/0324 hours) and 6 June 2012 (sunset/sunrise: 1946/0309 hours), between 2200 and 0215 hours local time. The test subjects were 46 territorial corncrake males randomly selected from the larger population. The study was conducted during the time of territory establishment by males, which is when males call most intensively, attracting the females that arrive at the breeding grounds a few days after the males (Green et al. 1997). The average temperature (measured between 2200 and 2300 hours at ground level) was  $9.7 \pm 5^\circ\text{C}$  (mean  $\pm$  SD).

#### Preparation of Call Stimuli

I used a total of 92 samples of natural broadcast calls recorded from 92 different males in 2008 within 7 days, about 200 km southwest. Both study site and the site of recording were a part of a continuous range; however, because males can move a few dozen kilometres during a season the chosen distance and time minimized the possibility of males listening to themselves and the potential effect of relatedness or previous contacts on their responses. All calls were digitally prepared to match a  $96 \pm 5$  dB signal pressure level (SPL at 1 m; natural amplitude) and randomly assigned to the following groups: training stimuli, monotonous rhythm stimuli, intermittent rhythm stimuli and natural rhythm stimuli.

#### Training stimuli

I manipulated the rhythm of 46 samples to create training stimuli, each lasting 290 s. Call rhythm was defined as the ratio 'I2/(S1+I1+S2)' (I1 = interval 1, S1 = syllable 1, I2 = interval 2, S2 = syllable 2; Fig. 1), with the higher values representing a more intermittent rhythm and the lower values a more monotonous rhythm. The stimuli were created in four steps: (1) samples were cut into  $10 \times 30$  s sections; (2) the rhythm of the first section was set to 0.85 and the 10th section to 0.42 by the extension or contraction of I2s, respectively. The rhythm of samples 2–9 was extrapolated linearly from the first and last sections so that rhythm was continually decreasing with time; (3) the sections obtained were shortened into final 20 s pieces; and (4) they were separated by  $9 \times 10$  s gaps of silence. The use of such a set-up was justified because it imitates the natural situation when males alternately call and become silent, most likely to locate the position of the calling intruder. Additionally, such a set-up prevented a strong overlap of calls (male and playback) on whole recordings, which could be problematic during the analysis of recordings.

#### Monotonous rhythm stimuli

I manipulated the rhythm of 16 samples to create monotonous rhythm stimuli (230 s; mean = 39, 36–42 syllables/20 s). The stimuli were created in four steps: (1) samples were cut into

$8 \times 30$  s sections; (2) the rhythm of all of the sections was set to 0.42 by the extension or contraction of I2s; (3) obtained sections were shortened into final 20 s pieces; and (4) the sections separated by  $7 \times 10$  s gaps of silence.

#### Intermittent rhythm stimuli

For intermittent rhythm stimuli (230 s; mean = 33, 32–34 syllables/20 s) I manipulated the rhythm of 15 samples in a similar way to the monotonous stimuli but used a rhythm of 0.85.

#### Natural rhythm stimuli

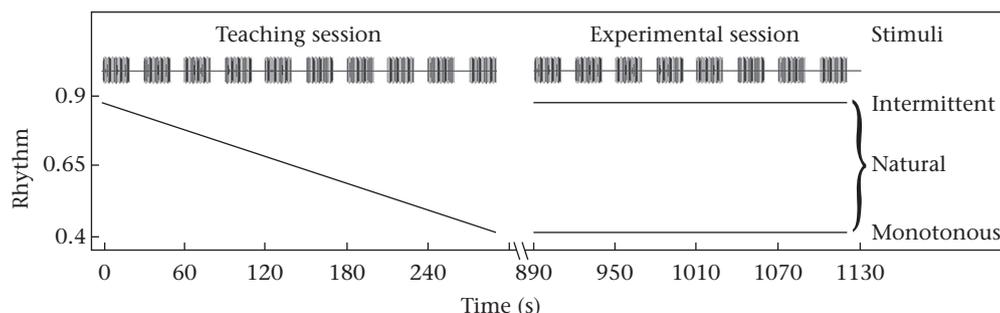
The remaining 15 samples maintained their natural rhythm (230 s; mean = 37, 34–40 syllables/20 s); however, the length of the playback was standardized in the same way as in monotonous and intermittent stimuli (i.e. call samples were trimmed into  $8 \times 20$  s sections, separated with  $7 \times 10$  s gaps).

Although the number of syllables played in each stimulus type was slightly different, a previous study (Ręk & Osiejuk 2013) proved that corncrakes respond specifically to the temporal patterns, not to the rate of calling. Therefore, it seems unlikely that this factor might be a reason for the differential responses to the different playback stimuli within the species.

#### Experiments and Treatments

I performed two experiments with the same design but used different stimuli (Fig. 2). All of the males received a training session and experimental session in this order (Fig. 2). Training sessions combined playback and movement stimulation, whereas experimental sessions involved only playback.

Before each trial, the experimenter holding the speaker was standing within the focal male's territory. When the playback began, the experimenter started to walk slowly towards the focal male until the beginning of the silent gap in playback (see description of Training stimuli and Fig. 2, above). After pausing during the silent gap, the experimenter continued to move towards the bird from that point. This sequence of playbacks and movements was repeated during the remaining nine playback sections of the training session. The rate of change in rhythm with time (Fig. 2) during the training session was within the natural range, whereas the change in the distance was set to match  $25 \pm 5$  m altogether. This value corresponds to the average distance covered by males during 5 min of playback (P. Ręk, unpublished data). Because the rhythm decreased with distance over consecutive playback sections, the males could associate changes in signalling with increasing aggressive motivation of the intruder (playback speaker). Corncrakes call within dense vegetation during the night. Therefore, it was practically impossible for the males to see the researcher, especially if the latter stopped moving during the gaps



**Figure 2.** The timeline of playback experiments and the scheme of acoustic stimulation. Trials consisted of a 290 s training session and a 240 s experimental session (including 10 s after the last playback), separated by a 10 min interlude.

of silence between playbacks. After the last playback section of the training session, the speaker was turned off for 10 min.

During the experimental session, the speaker was motionless and playback started from the position where it had finished during the training session. The training playback and experimental playback each contained the calls of a single male, but the males of the training playback and experimental playback heard by a focal individual were different. Because in natural conditions males interact frequently with several competitors within the same time period this represented a naturally occurring situation.

In experiment 1 (E1;  $N = 31$  trials with 31 males), I tested the responses of the receivers from two independent treatment groups to two different types of acoustic stimuli: with a monotonous rhythm of calls ( $N = 16$ ) or with an intermittent rhythm of calls ( $N = 15$ ). I analysed how the aggressive behaviour of males was influenced by the rhythm level of the intruder male's calls after training (i.e. whether males comprehended a difference between the patterns after training).

In experiment 2 (E2;  $N = 15$  trials with 15 males), males received natural rhythm stimuli after training sessions. I observed the behaviour of senders, in relation to the rhythm of their calls (i.e. whether males still used the natural strategy of signalling (see below) or the just trained strategy). Because inferring signal function based solely on the signal broadcast on a subject's territory (E1) can be inconclusive (Searcy & Beecher 2009), this analysis was to provide further insight into the signal function after the training session and to depict more precisely a male's behaviours in the context of his own vocal signals (Hurd & Enquist 2001). In E1, the function of the playback was to demonstrate differential response to the intermittent versus monotonous signal, whereas in E2, the function of the playback was only to mimic the presence of the intruder. Therefore, these two pieces of evidence should be treated independently.

For the playback experiments, I used a Creative ZEN player (quality of files: PCM, 48 000 Hz, 16 bits) with a wireless SEKAKU WA-320 (Taichung, ROC Taiwan) loudspeaker with 20 W amplifier and 50–15 000 Hz frequency range. All of the experiments were conducted within an acoustic location system (ALS), which consisted of an array of four omnidirectional microphones (Sennheiser K6/ME 62) recording to an Edirol R-4 Pro 4-channel Portable Recorder and Wave Editor (sampling frequency 48 kHz, 16 bit resolution). Microphones were fixed at 1.5 m above the ground. The use of the animals adhered to ethical guidelines for animal research in Poland and was approved by the Adam Mickiewicz University Ethics Board (no. 2011/03/D/NZ8/02133).

#### *Data on the Natural Signalling Strategy of Males*

The interpretation of the results is based on the statement that the escalation (decrease in distance) of a territorial conflict by males is associated with a gradual change towards a more aggressive-intermittent rhythm, whereas a retreat corresponds with a gradual change towards a more submissive-monotonous rhythm. To support this assumption I present data from 20 trials ( $N = 20$  males) collected in Kampinoski NP (about 200 km south-west from the study area; 20°23'E and 52°19'N; ca. 24 km<sup>2</sup>) between 17 and 28 May 2007. These trials did not include a training session and were used only to illustrate the natural signalling strategy of males (change in rhythm with distance to the intruder) during territorial interactions. Furthermore, they had the same design and were carried out and analysed identically to the experimental sessions from E2.

To show that the difference between the responses of males from 2007 and 2012 were not caused by the year or study site but by the training stimulation, I additionally present the data on

rhythm and distance to the speaker straight after the initial 20 s of playback stimulation in both periods (i.e. after the first 20 s section of playback stimulation during training sessions in the 2012 trials and after the first 20 s section of playback stimulation in the 2007 trials). At this very initial stage of interactions, males' responses are still relatively spontaneous and depend more on the initial state of the male rather than on the specific parameters of the stimuli. Therefore, they should reflect the natural signalling strategy of crows on a short timescale. Unless year or site affected males' way of signalling, rhythm should be negatively correlated with distance to the speaker, regardless of the period.

#### *Data Analysis*

The use of ALS for an objective measurement of subjects' positions and movements enables a continual record of an individual's behaviour during the trial. I used the acoustic locator algorithm in XBAT (v. 0.6.1, Cornell Lab of Ornithology, Ithaca, NY, U.S.A.) to determine the position of focal subjects within the microphone array. If the subject bird was calling, I used the acoustic locator to determine the position of both the bird and the speaker. If the subject bird was quiet but moved, his position was visually mapped and the speaker was acoustically located.

To make use of such data, in E1 I used an index that comprehensively quantifies a male's behaviour throughout the trial, also known as the mode of approach (MA). This index enables the quantification of complex behaviours such as encircling. Its suitability was assessed in this species and it was proven that the pattern it describes is not artificially generated by the transformation of the original data (Ręć & Osiejuk 2010, 2013). MA is given by the formula:

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

where  $s$  = time section of experimental session (1–8 = during consecutive silence gaps and during 10 s interval after last playback; see Fig. 2),  $d_b$  = distance to the speaker before the section,  $d_a$  = distance to the speaker after the section and  $d_r$  = the real distance covered.

The score is based on the transformation of the distance measures ( $d$ ) into the angle of approach, in such a way that the smaller the angle the more direct the approach towards the speaker. Therefore, a male moving directly towards the speaker would have an MA of approximately 0; lower or higher values than 90 indicate that a bird is moving towards or away from the speaker, respectively. In addition, this measure includes a correction for distance ( $\log_9 d_a$ ) that is important because of some restrictions to motion during experiments (see Ręć & Osiejuk 2013 for more details).

In E2, I calculated rhythm of calls and I used the data from ALS to calculate the distance of males to the speaker throughout the trials. Distance and rhythm values used in calculations were means from seven consecutive silence gaps and from the 10 s interval after the last playback. Within each of these silent phases the rhythm was calculated based on 20 consecutive syllables.

#### *Statistics*

I used a  $t$  test to analyse the MA data from E1. I tested the effect of the playback treatment (intermittent versus monotonous) on the behaviour of the receivers. I also used Fisher's exact tests to compare the numbers of males that listened to the monotonous or intermittent playback and approached or did not approach within 2 m of the speaker. This test was used because two of four expected

values in the contingency table were below 10. In E2 I tested the effect of the distance to the speaker on the rhythm of the males. Next, I compared this effect with the same behaviour in males tested in 2007 using the GLM module of Statistica (2007; v 8.0, StatSoft, Tulsa, OK, U.S.A.). To normalize residual distributions and achieve a linear pairwise relationship, the distance was log transformed. All *P* values are two tailed.

## RESULTS

### *Comprehension of New Temporal Pattern*

In E1, I tested whether males receiving training with a new code would comprehend the new association between the temporal pattern of calls and approaching behaviour of the intruder during the subsequent interaction. After the training session, males approached the playback speaker significantly faster and more closely (lower MA score) when playback was monotonous than when it was intermittent (Fig. 3a;  $t_{29} = 2.52$ ,  $P = 0.018$ ). Similarly, a higher proportion of the males that listened to the monotonous playback approached within 2 m of the speaker than those males that listened to the intermittent playback (Fig. 3b; Fisher's exact test:  $P = 0.029$ ), although males in the two treatment groups moved similar distances (Fig. 3c;  $t_{29} = 0.31$ ,  $P = 0.760$ ).

### *Copying and Usage of New versus Natural Signalling Strategy*

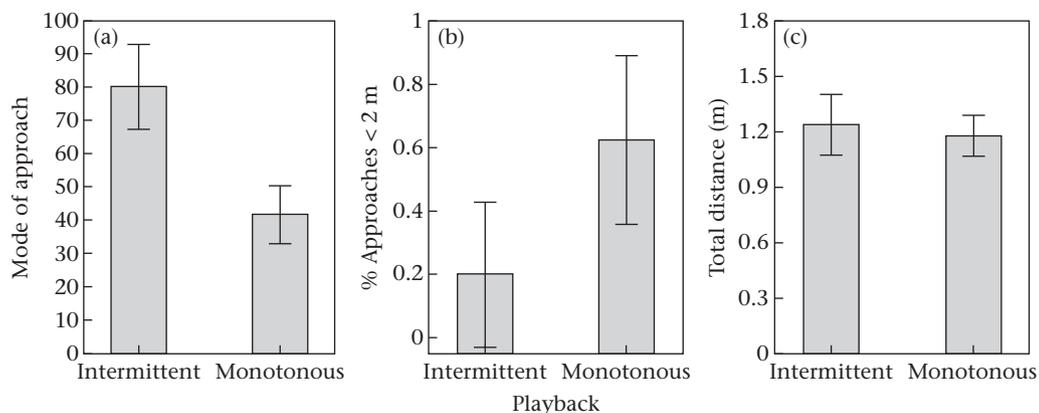
Before any stimulation, males from E1, E2 (2012) and 2007 were calling with similar rhythm (E1: mean  $\pm$  SE =  $0.78 \pm 0.03$ ; E2: mean  $\pm$  SE =  $0.74 \pm 0.04$ ; 2007: mean  $\pm$  SE =  $0.71 \pm 0.03$ ; ANOVA:  $F_{2,63} = 1.32$ ,  $P = 0.275$ ). In 2007, the closer the males were to the speaker the higher the rhythm of their calls ( $r = -0.46$ ,  $P = 0.038$ ; Fig. 4a). Similarly, in the initial stages of interactions in 2012 and 2007, males were calling with higher rhythm the closer they were to the speaker (Fig. 4b, d). Although these correlations were not significant (2012:  $r = -0.14$ ,  $P = 0.449$ ; 2007:  $r = -0.13$ ,  $P = 0.596$ ), the slopes of the rhythm functions were relatively high considering their short timescale with only one playback section, compared with the full-scale trials with eight playback sections (Fig. 4). This supports the assumption that the natural signalling strategy involved the increase of rhythm by a male while approaching the intruder.

By contrast, males receiving a training session had a lower rhythm the closer they were to the speaker during experimental sessions with the natural rhythm playback (E2;  $r = 0.65$ ,  $P = 0.008$ ;

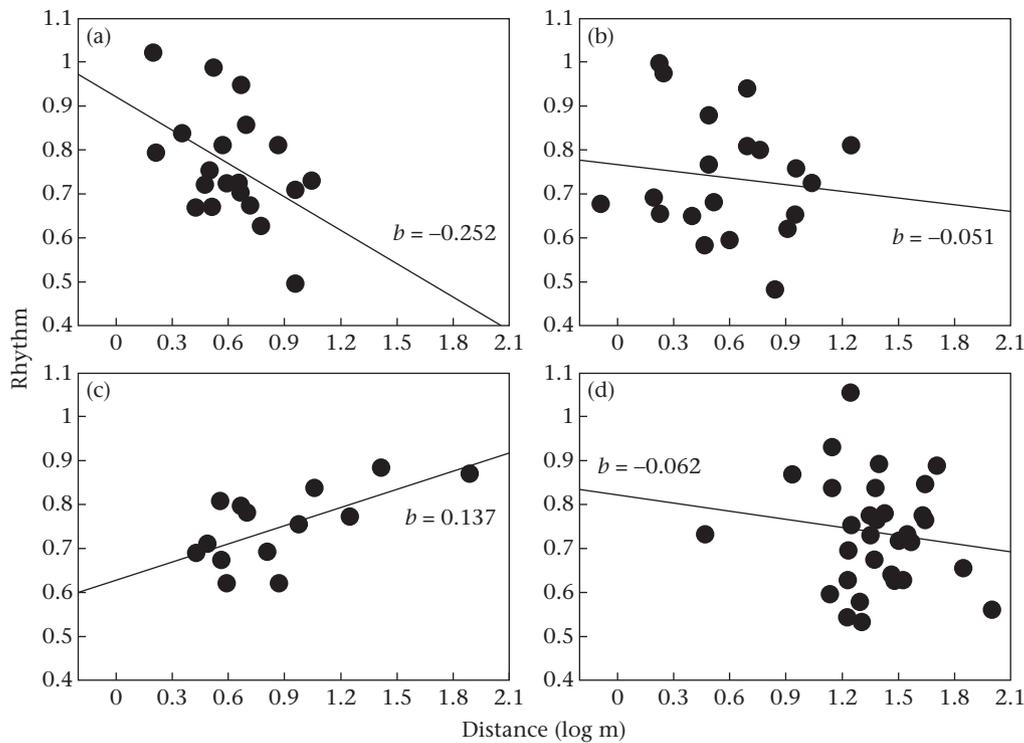
Fig. 4c). This increasing trend was significantly different from the decreasing trend in 2007 (Table 1), indicating that males learned to call more monotonously while approaching the intruder. Moreover, the rhythm was significantly higher (more intermittent) in 2007 than in 2012 (2007: mean  $\pm$  SE =  $0.76 \pm 0.03$ ; 2012 E2: mean  $\pm$  SE =  $0.74 \pm 0.02$ ); however, considering the natural range of corncrake rhythms (0.4–1.2), this difference was relatively small.

## DISCUSSION

This paper addressed whether male corncrakes, nonpasserine birds generally considered to be a nonlearning species, are able to learn new associations between temporal patterns of their calls and meanings and to use temporal patterns in a different context. The results of my experiments demonstrate that males were able to comprehend a new code after only a few minutes of exposure to the code. Additionally, apart from understanding, males acquired a new signalling strategy; they began signalling their aggressive motivation with a new pattern. These results indicate that corncrakes' innate call structures and lack of the complex and variable songs of song-learning passerines allow them to learn the timing of calls. It should be emphasized, however, that the learning of a new meaning was shown on a single response after one learning bout. Therefore, it is not clear whether this really changed the meaning for all subsequent interactions or only changed the motivation within this specific situation. Moreover, based on the results from E1, it might be concluded that males responded more intensively to monotonous than to intermittent rhythm in experimental session of E1 not because rhythm decreased with decreasing distance during training session but because monotonous rhythm was the last rhythm they heard. While such a conclusion is consistent with the results of E1, it contradicts the results of E2. There is no reason why males from E2 should change their way of signalling as they did only if the last rhythm heard a few minutes earlier was monotonous. Finally, it appears surprising that 5 min of learning was sufficient to change the code of a signal commonly used during a whole breeding season, or even a whole life. Nevertheless, most likely this process has very little if anything in common with the long-lasting vocal learning process of passerines and rather more with a simple learning process based on conditioning that has proved to be rapid in many groups of animals. Hence, the possible implications of this ability for the evolution of communication systems in animals with small repertoires of vocalizations are even more intriguing than its mechanism. So the next step should be to focus on the natural acquisition of this ability, to back up these data.



**Figure 3.** Reactions of males to two different playback stimuli after training session of E1 (mean  $\pm$  SE): (a) mode of approach (in arbitrary units approximately equivalent to degrees); (b) proportion of males' approaches to less than 2 m from the playback speaker; and (c) total distance covered during a trial (experimental session). Lower values of mode of approach score (a) and higher proportions of approaches (b) indicate stronger reactions.



**Figure 4.** Changes of rhythm with distance to the speaker: (a) among males receiving only natural rhythm stimuli (2007); (b) immediately after the initial 20 s of playback stimulation during 2007 trials; (c) among males receiving training with contradictory signal before playback with natural rhythm stimuli (E2, 2012); and (d) straight after the initial 20 s of playback stimulation during training sessions of 2012 trials. The  $b$  values are slopes of linear functions.

The phenomena described in this study involved the comprehension of a new association between the signal and its meaning. However, the described phenomena concerned the order of song elements instead of song elements themselves. In fact, the communication system of the corncrake is based on the relative distribution of vocalizations and intervals (Reĳ & Osiejuk 2013). Such patterns can make the association between signal elements and aggressive motivation very flexible for cultural transmission via vocal communication, because in contrast to acoustic features, which are likely to be constrained by anatomy and therefore have a genetic basis (Fitch & Hauser 2003), syntactic patterns could be genetic or cultural (Kershenbaum et al. 2012). Birds can learn to discriminate among a wide variety of sounds and respond differently to them (Adret 1993; Janik & Slater 1997). Nevertheless, from an evolutionary perspective, the flexibility of responses to auditory stimuli is limited because not all associations between the signal and its meaning are equally likely. With the lack of arbitrariness of the signal, its function is constrained and conditional upon the acoustic structure of the signal, which decreases the flexibility of associations by making some associations evolutionarily unstable and others adaptive (Guilford & Dawkins 1995; Gil & Gahr 2002; Maynard Smith & Harper 2003). This is a factor, apart from learned or innate dichotomy, that must be considered when analysing the degree of flexibility in vocalization comprehension, unless the meaning of a signal is strictly referential or symbolic (Zuberbühler 2003; Arnold & Zuberbühler 2008; Ouattara et al.

2009). Any reliable information regarding the sender, especially in an antagonistic interaction, is useful to a receiver. Therefore, a receiver's ability to learn new associations based on a sender's behaviour appears to be an advantageous strategy, provided the cost of learning does not exceed the eventual benefits. The cost here means that the receiver should not respond to a new association if there is no stable mechanism ensuring its reliability. Considering these limitations, syntactic patterns appear to be especially convenient material for the formation of new signals (Hurford 2011).

In addition to comprehending the new code, corncrakes used it during the subsequent interaction. Therefore, a limited call repertoire might provide listeners with a wider set of meanings than originally proposed (Osiejuk et al. 2004). Many experiments on songbirds and mammals suggest that context-specific vocal usage can be acquired through experience (Kroodsma 1988; Spector et al. 1989; Cheney & Seyfarth 1992; Hollén et al. 2008); however, most animals use specific call types only in a limited range of contexts. In songbirds, for example, context-specific vocal usage (e.g. matching, overlapping, switching) seems adaptive because it enables males to negotiate over territory boundaries and to better compare with each other (Collins 2004; Bradbury & Vehrencamp 2011). In corncrakes, the rhythm of calls serves as a territorial broadcast signal (Reĳ & Osiejuk 2010). However, because rails usually communicate over large distances, syntactic patterns may be less susceptible to degradation than the acoustic structure of vocalizations, and therefore may be more reliable as territorial signals. At the same time, because rails' call repertoires are relatively small and genetically constrained, the ability to adjust different temporal patterns to different social contexts can be less costly than the development of new vocalizations (Nowicki et al. 1998; de Kort & ten Cate 2004; Spencer et al. 2004). Nevertheless, little is known about the geographical distribution of syntactic patterns and even less is known about the distribution of pattern-meaning pairs in the

**Table 1**  
Separate slopes ANCOVA model with rhythm as a dependent variable

|                  | $F$   | $df$ | $P$   | Partial $\eta^2$ |
|------------------|-------|------|-------|------------------|
| Stimuli†         | 11.18 | 1    | 0.002 | 0.265            |
| Stimuli*distance | 5.72  | 2    | 0.008 | 0.270            |

† Males subjected to training plus experimental sessions versus males subjected only to experimental sessions.

corncrake. It is not clear to what extent the acquisition of pattern-meaning pairs is associated with contextual learning that requires the use of innate patterns or with learning of patterns.

Unlike humans, the majority of animals have repertoires of songs or calls that are relatively small and static during development. However, the communication system of the corncrake may have one similarity with human language. In the asymmetric system of the corncrake, which has a small repertoire of relatively fixed calls that can be distributed temporarily in an open-ended way, learning appears to be age-independent or, at least, the majority of males appear able to learn. It relies on connecting syntactic patterns of calls and meanings rather than vocalizations and meanings. Further investigation is required to determine whether corncrakes select signals only from an innate repertoire of temporal patterns without production learning being involved or are indeed capable of copying and generating novel temporal patterns, where new signals (not only new associations) are acquired as a result of experience (Janik & Slater 2000).

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