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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.

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.

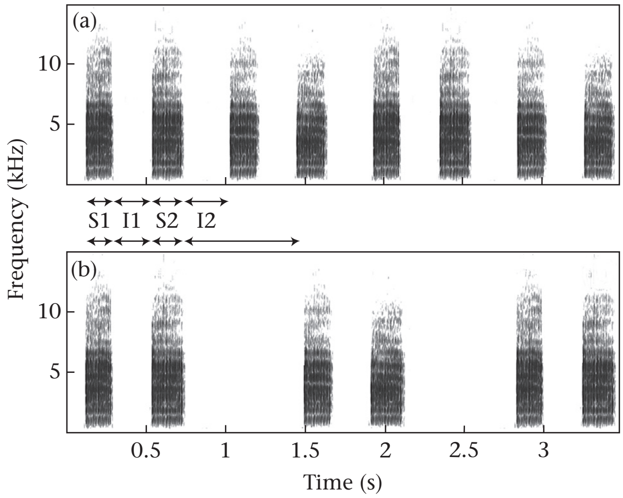

Figure 1. Sonograms of corncrake calls: (a) broadcast call with a monotonous rhythm; (b) broadcast call with an intermittent rhythm. The rhythm of the broadcast calls was defined as the ratio of the length of the second interval (I2) to the sum of the lengths of the first syllable (S1), first interval (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.

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 abovementioned 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