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No male identity information loss during call propagation through dense vegetation: The case of the corncrake

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ABSTRACT

Individually specific acoustic signals in birds are used in territorial defence. These signals enable a reduction of energy expenditure due to individual recognition between rivals and the associated threat levels. Mechanisms and acoustic cues used for individual recognition seem to be versatile among birds. However, most studies so far have been conducted on oscine species. Few studies have focused on exactly how the potential for individual recognition changes with distance between the signaller and receiver. We studied a nocturnally active rail species, the corncrake, which utters a seemingly simple disyllabic call. The inner call structure, however, is quite complex and expressed as intervals between maximal amplitude peaks, called pulse-to-pulse durations (PPD). The inner call is characterized by very low within-individual variation and high between-individuals difference. These variations and differences enable recognition of individuals. We conducted our propagation experiments in a natural corncrake habitat. We found that PPD was not affected by transmission. Correct individual identification was possible regardless of the distance and position of the microphone which was above the ground. The results for sounds from the extreme distance propagated through the vegetation compared to those transmitted above the vegetation were even better. These results support the idea that PPD structure has evolved under selection favouring individual recognition in a species signalling at night, in a dense environment and close to the ground.

1. Introduction

Vocal territorial behaviour enables birds to reduce the costs of defending resources. It is advantageous because in a stable social situation birds may adjust their territorial behaviour towards rivals that differ in level of threat (Searcy and Beecher, 2009). For example, an established neighbour is less of a threat than a stranger and therefore does not require a strong response (the so called 'dear enemy' effect; Trivers, 1971; Temeles, 1994). Differential responses are only possible if signals are individually specific and if receivers are able to discriminate between them.

Individual recognition based on acoustic signals is widespread in birds, but cues and mechanisms underlying it are diverse and are still under debate (Stoddard, 1996). Many species have song repertoires and repertoire differences are a good candidate for common recognition cues (Stoddard et al., 1991). Song types are often shared among individuals within a local population, which may negatively affect discrimination. Therefore, it was suggested that cues used for individual recognition could be related to song features other than repertoire (Lambrechts and Dhondt, 1995; Skierczyński et al., 2007; Skierczyński and Osiejuk, 2010). This could be especially important for birds in which vocal learning is not required for development and production of normal song. Indeed, individual discrimination was also shown in suboscine passerines, which have simpler vocalizations that are not culturally transmitted (Lovell and Lein, 2004a,b). In non-passerines, individual recognition seems to be common among species breeding in colonies (e.g. Evans, 1970; White, 1971; Jouventin, 1982; Robisson et al., 1993; Aubin and Jouventin, 1998), and especially for parent–chick recognition (Seddon and VanHezik, 1992; Lengagne et al., 2001). Individuality in acoustic signals was also found in territorial non-passerines communicating at greater distances, e.g. in owls (Galeotti and Pavan, 1991; Delport et al., 2002; Dragonetti, 2007) or bittern *Botaurus stellaris* (McGregor and Byle, 1992). Less is known about how different sound structures may encode individuality and, especially, how the potential for individual recognition changes with an increase in the distance between sender and receiver. In this study, we focused on how distance affects call structure responsible for individual recognition in nocturnally signalling rail species.

The corncrake *Crex crex* (Rallidae) has a very characteristic, loud cracking call, which is uttered by males during the breeding season. Their call is considered as a functional equivalent of a songbird's song, functioning as a signal deterring rivals and attracting mates (Cramp and Simmons, 1980; Green et al., 1997). This call

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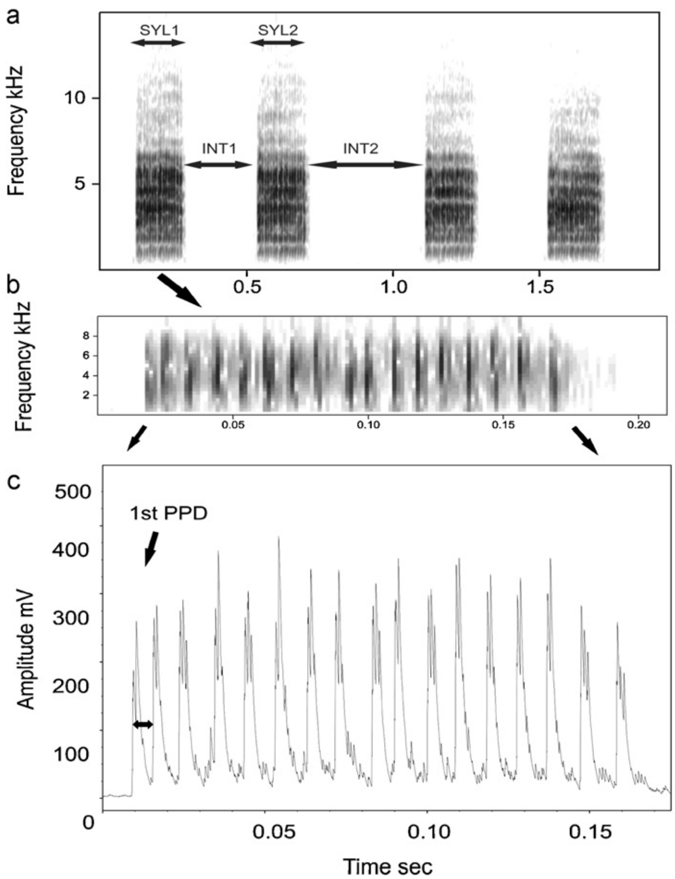

Fig. 1. Sonogram of a corncrake *Crex crex* call. (a) A typical sequence of calls with two syllables (SYL1 and SYL2) and intervals (INT1 and INT2). Enlarged is SYL1 with the structure of the pulses visible. (b) An envelope of SYL1 showing pulse-to-pulse duration (PPD); a feature used for discriminating between individuals.

appears very simple, as there is no repertoire variation, especially when compared to the elaborate songs of passerines. It consists of two similar units slightly different in duration (syllables SYL1 and SYL2, Fig. 1) organised in a stereotypical manner, and repeated thousands of times at night (Green et al., 1997). Recently, it was experimentally demonstrated that the corncrake males signal their neighbours about their aggressive motivation by modifying call rhythm (Ręk and Osiejuk, 2010). The corncrake call is a structurally toneless, repeated pulse signal. The inner call structure, expressed as intervals between maximal amplitude peaks (called pulse-to-pulse duration or PPD), was shown to be individually characteristic and invariable over long periods (May, 1998; Peake et al., 1998; Peake and McGregor, 2001). The results of the above mentioned studies revealed that PPD structure enables individual recognition and might be useful for conservation purposes because it allows for monitoring individually known males. However, an important question has remained unanswered, namely, how identity information encoded in PPD structure changes during signal propagation? Typically, corncrakes call from ground level in a dense wet meadow habitat. This means that there are many obstacles able to strongly influence their calls. It could also mean that their calls may suffer from the ground effect (when signaller and receiver are close to the ground there is interference between sound propagating directly from signaller to receiver and sound reflected to the ground – Wiley and Richards, 1978,1982). Nevertheless, their calls are the only kind of signal corncrakes may use for information exchange at night. The aim of this study was to test how information about individual identity encoded in the structure of corncrake calls is transmitted through the acoustical environment of wet meadows. We predict that if PPD structure is responsible for individual discrimination processes, it should remain relatively stable after propagation over typical distances separating territorial males. An experimental test of individual recognition with non-degraded and degraded signals will be the subject of a separate study (in prep.).

2. Materials and methods

2.1. Study area

The sound propagation experiment was carried out in the western part of the Kampinoski National Park (central Poland, 20°23′31″E, 52°19′26″N) on 14 May 2008. The whole study plot (ca. 24 km^2), called 'Farmułowskie Meadows' is an open swampy area between two inland dune systems. The area consists of a mosaic of peatland, wet meadows and a small proportion of formerly arable land at an early stage of succession. The area is naturally closed in from the north, east and west by forests, which ensures stable breeding conditions. In this area, corncrakes prefer vegetation patches dominated by larger sedge species e.g. *Carex gracilis* or *C. acutiformis* (60% of cracking males), wet unmowed meadows (20%), reed beds composed of common reed *Phragmites australis* (5–10%) and communities dominated by nettle *Urtica dioica* (2–8%). Few males were noticed in other types of vegetation, such as grasslands or pastures (2–4%). The population of corncrake in the study area usually exceeds 50 males (Osiejuk et al., 2004; Ręk and Osiejuk, 2010).

A loudspeaker and microphones were located along a 100 m long transect crossing a uniform patch dominated by sedges (height 60–120 cm), i.e. vegetation preferred locally by corncrakes. A year earlier at this location we had observed and recorded 4 corncrake males, and in 2008 we conducted experiments just before the spring settlement.

2.2. Propagated sounds

As a model for the corncrake calls, we chose a series of 10 calls (i.e. 20 syllables) of seven different individuals recorded from the same population one year earlier. The series of calls were chosen from a larger set of recordings based on their quality. We used calls recorded at a short distance (<5 m) and with a minimal amount of background noise in order to minimize propagation-induced modification. Sonogram analysis revealed that any propagation-induced degradation, such as tailing effects at the end of the signal or smearing effects on the frequency and amplitude modulated parts, was practically absent. Males were recorded with Edirol R-4 Pro 4-channel Portable Recorder and Wave Editor (Hamamatsu, Japan) and Sennheiser ME 62 microphones with windscreen.

2.3. Transmission experiments

To assess the modifications of signals during propagation through the natural habitat, each of the seven series of calls was broadcasted repeatedly and recorded at different heights and distances. The test sequence consisted of seven males call series separated by silence. We broadcasted all the signals at a 96 dB SPL measured at 1 m from the loudspeaker. This value corresponds to the natural amplitude of a calling corncrake. This natural amplitude was measured earlier for several males calling at known and small distances (<10 m) with a CHY 650 (Ningbo, China) sound pressure level meter.

Two different experimental trials were executed. For the first 'low' trial, both speaker and microphones were placed 25 cm above ground level. This is the typical position of corncrakes when calling and receiving signals. The three microphones for recording the propagated signals were placed at 25 m, 50 m and 100 m from