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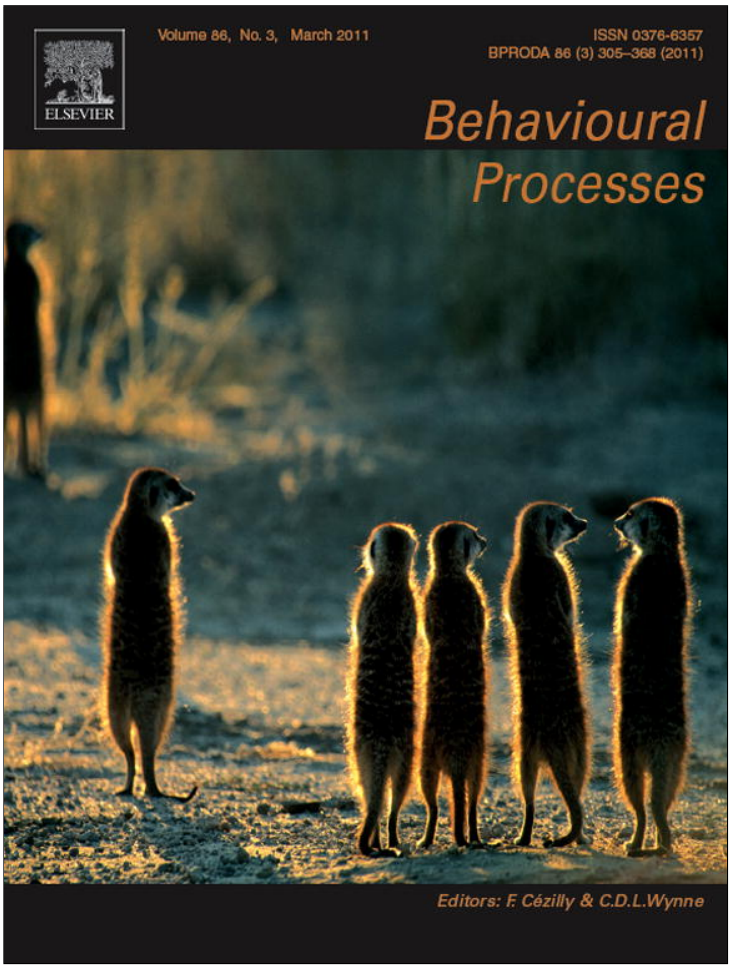

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No male identity information loss during call propagation through dense vegetation: The case of the corncrake

Paweł Ręk, Tomasz S. Osiejuk*

Department of Behavioural Ecology, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland

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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.

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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

* Corresponding author.
E-mail address: t.s.osiejuk@life.pl (T.S. Osiejuk).

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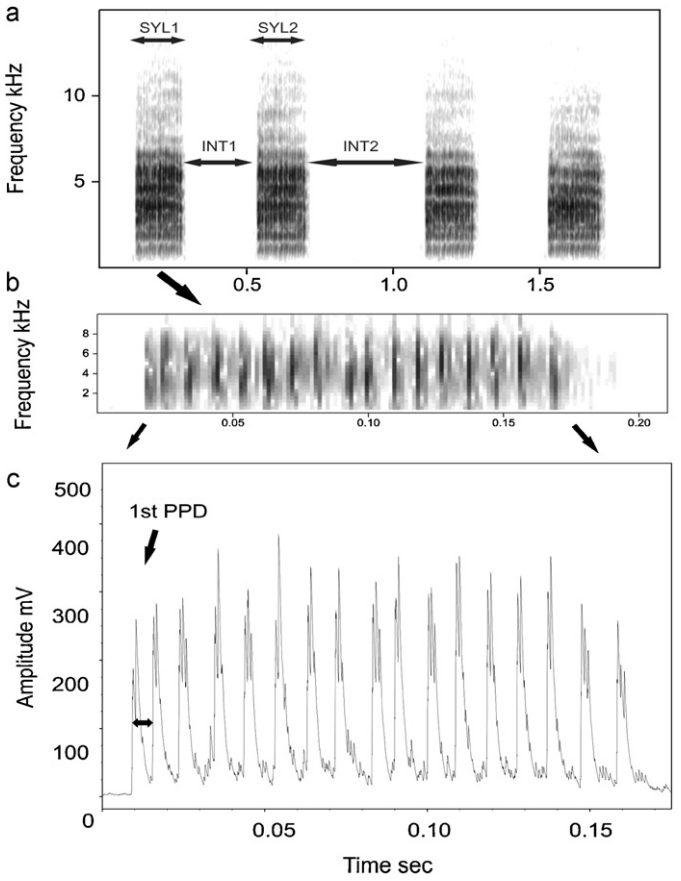

Fig. 1. Sonogram of a corncrake *Crex crex* call. (a) A typical sequence of calls with two syllables (SYL1 and SYL2) and intervals (INT1 and INT2). Enlarged is SYL1 with the structure of the pulses visible. (b) An envelope of SYL1 showing pulse-to-pulse duration (PPD); a feature used for discriminating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

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the loudspeaker. For the second 'high' trial we positioned the microphones at a height of 250 cm above ground level so that the transmitted sound spreads over the vegetation level, which never exceeded 120 cm in our experiment. Calls recorded with microphones are from here onwards referred to as 'propagated sounds'. During both trials an additional fourth microphone was placed in an open area at 1.56 m from the loudspeaker to record 'control sounds' to be compared with the 'propagated sounds'. As we did not find any significant difference between control sounds from the low and the high trial, we only used control sounds from the low trial.

Corncrake calls are very loud and could be heard from a distance of up to 1–1.5 km (Schäffer and Koffijberg, 2004). However, our earlier playback experiments with the species revealed that males respond to playback if the distance to the loudspeaker is relatively close (Ręk and Osiejuk, 2010). It is hard to attract a male to a playback conducted from a distance of over 50–100 m, which suggests that high amplitude of calls could be important for attracting mates. Additionally, analysis of mapped territories of hundreds of males (data from Osiejuk et al., 2004) indicated that the number of direct neighbours rarely exceeds five. Therefore, we chose 25 m, 50 m and 100 m distances to play back calls of seven males. We assumed that this is a good reflection of the natural situation in which a male may simultaneously hear a few neighbours and also some strangers potentially invading his territory. The male will adjust response strength when discriminating between neighbours and strangers.

Signals were emitted by a Marantz PMD 670 solid state recorder connected to a SEKAKU WA-320 (Taichung, ROC Taiwan) loudspeaker with a 20 W amplifier (frequency range 50–15,000 Hz and linear frequency response within species-specific frequency range). Recordings of propagated and control sounds were made with four omnidirectional Sennheiser ME 62 microphones (frequency response: 150–15,000 Hz, 2 dB) connected to a Edirol R-4 Pro 4-channel Portable Recorder and Wave Editor (Hamamatsu, Japan) (sampling frequency 48 kHz, 16 bit resolution, linear response within the range of 20–20,000 Hz).

Weather conditions (at 1 m height) were monitored by a wireless digital weather station (Oregon Scientific WMR 928, accuracy for temperature 0.1 °C and for humidity 1% RU, for pressure 100 Pa and for wind speed 0.2 m/s). Both propagations were done on 14 May 2008 between 21:45 and 22:10 local time (GMT + 1). During the experiments the temperature decreased from 3.5 to 2.7 °C, humidity increased from 81% to 84%, air pressure (1011 hPa) and wind speed (0 m/s) were stable.

2.4. Data analysis

The propagated sounds and the model sounds were analysed with Avisoft SASLab Pro 4.52 (Specht, 2007) at 48 kHz/16 bit PCM files. The main aim of the analysis was to compare the individual variation in the PPD structure, between control and propagated sounds. In order to measure PPD objectively we used the 'Pulse Train Analysis' function. The general settings of the sonogram window were as follows: FFT = 256, frame % = 25, Hamming window, bandwidth 975 Hz, frequency resolution = 188 Hz and temporal resolution = 98.43. These settings make measurements in time domain with 0.0833 ms accuracy possible. Prior to the analysis, all sounds were high-pass filtered (500 Hz) with FIR Time Domain Filter. This procedure enabled removal of irrelevant low-frequency noise, which may affect detecting envelopes. We used the 'rectification + exponential decay' method for envelope detection and in each measurement of pulse distribution we visually checked if all pulses were detected. For the Pulse Train Analysis we initially started measuring with the following settings: time constant = 1 ms, threshold = 0.05 Pa, hysteresis = −14 dB, start end threshold = −10 dB. However for the propagated sounds recorded at over a 25 m distance we had to decrease threshold and to manipulate hysteresis between −14 and −10 dB in order to detect all pulses.

2.5. Statistics

We used discriminant analysis with a cross-validation procedure to find out to what extent PPD measures enable discrimination between syllables belonging to different males. We used PPD values for both syllables, as there was no significant difference between PPD distribution for SYL1 and SYL2 of particular males. The only difference concerned the number of pulses. There were a larger number of pulses for SYL2 than for SYL1. It is known, however, that values of PPD are repeatable for a male only for the first part of each syllable. The closer to the syllable end, the more individually variable they become which probably results from the mechanism of production (Peake et al., 1998). In order to check how PPD variation reflects ability for individual recognition in our sample of calls, we first conducted several discriminant analyses with different numbers of PPD included. As the shortest syllables in our sample had 16 pulses we were able to incorporate maximally 15 PPD to include all calls into a single analysis. In subsequent analyses, we compared PPD variation at each distance and height combination. Comparison was necessary in order to check how the potential for individual recognition changes with distance during propagation. We used coefficients of variation (CV) of PPD measurements to compare potential for individual coding between different distances of sound propagation and heights of the microphone. Coefficients of variation for mean values of each PPD were calculated for each individual and each distance and height combination (CV_i). The inter-individual coefficients of variation (CV_b) were calculated using mean PPD values from each individual (calculated separately for each distance and microphone height). Then ratios CV_b/mean CV_i were calculated. The ratios over 1.0 indicate that measurements (here following PPD) vary more between individuals than within individuals and thus have a potential for individual coding (Aubin et al., 2004). Finally, differences between distances or height in CV_b/mean CV_i ratios were tested. All the above-mentioned statistic analyses were conducted with SPSS 16.0. We used a multilevel mixed-effect model to analyze the effect of distance and microphone height on PPD with a xtmixed procedure of STATA/SE 11.0 for Mac. In the above analysis we include male and number, of each of the 15 PPD included for each call, as random factors.

3. Results

3.1. Informative value of pulse-to-pulse duration variation

We found that measurements of the PPD structure of model sounds provided for a very efficient discrimination between males. Even single, first PPD allowed for the correct classification of 43.6% of the syllables in a cross-validation procedure of discriminant analysis. The more PPD measurements we added the better the results obtained (Fig. 2). In subsequent analyses we used all 15 measures of PPD, which enabled the correct discrimination of 97.1% of the syllables for model sounds. As few as the first five PPD, however, enabled discrimination at a level exceeding 90% (Fig. 2). The coefficient of variation analysis revealed that CV_b/mean CV_i ratios always exceeded 1.0. The ratios varied between 1.41 and 8.16 depending on how many PPD, and depending on which distance, and which microphone height was taken into account.

3.2. Pulse-to-pulse duration changes during propagation

When the first 15 PPD values were used in discriminant analyses, the percentages of correctly classified syllables for all distances

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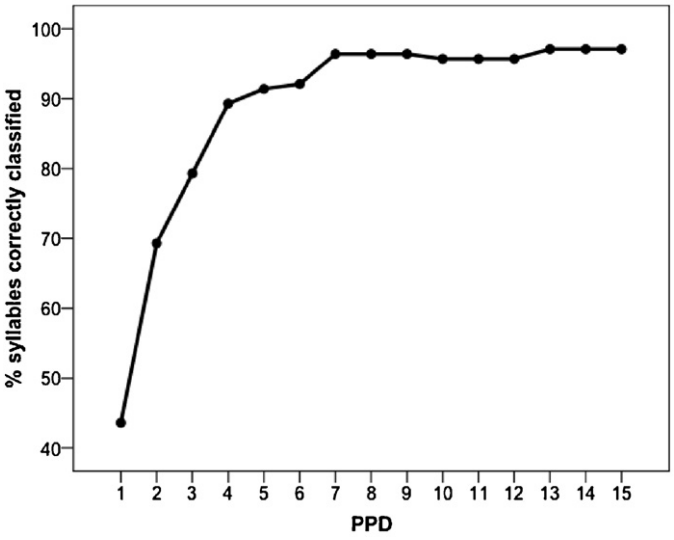

Fig. 2. Percentage of correctly classified syllables in a cross-validation procedure of discriminant analysis. Sequences of 1–15 PPD measurements were included in subsequent analyses.

from 25 to 100 m were high and varied between 93.6 and 97.9% (Fig. 3). We found that the discrimination of propagated sounds was slightly better (1.4–2.8%; Fig. 3) at 25 and 50 m for sounds recorded at 250 cm compared to those recorded at 25 cm above ground level. For the propagated sounds recorded at a 100 m distance, discrimination was better for sounds recorded at 25 cm above ground level than for those recorded at 250 cm (difference 4.3%; Fig. 3). We tested differences in potential of coding identity between different microphone heights for each propagation distance, with paired t-test where CV_b/mean CV_i ratios for each of 15 PPD was included. We found that at 25 m the potential of coding identity was significantly higher for propagated sounds recorded at 250 cm compared to those recorded at 25 cm above ground level ($t = -3.266$, $p = 0.006$; Fig. 4). There was no significant difference for propagated sounds recorded at different heights at 50 m ($t = 0.542$, $p = 0.596$; Fig. 4).

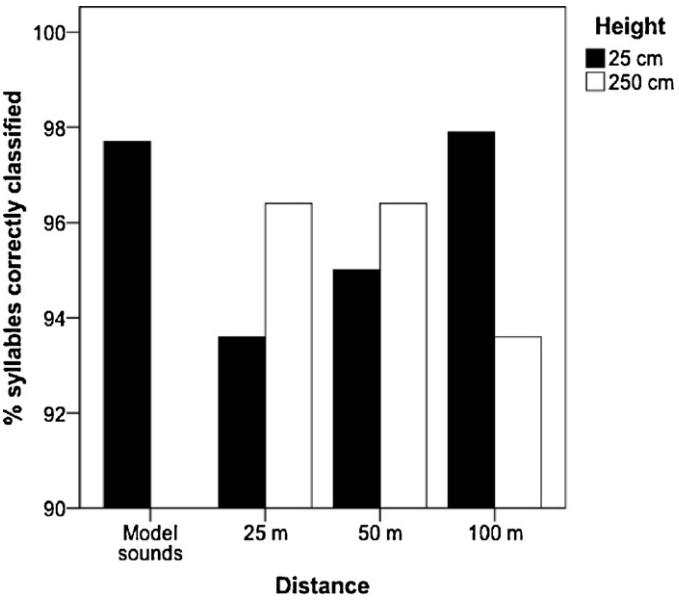

Fig. 3. Percentage of correctly classified syllables in a cross-validation procedure of discriminant analysis. Separate analyses were conducted for model sounds and propagated sounds, recorded at a 25, 50 and 100 m distance from a loudspeaker and at different microphone heights above the ground (25 cm and 250 cm).

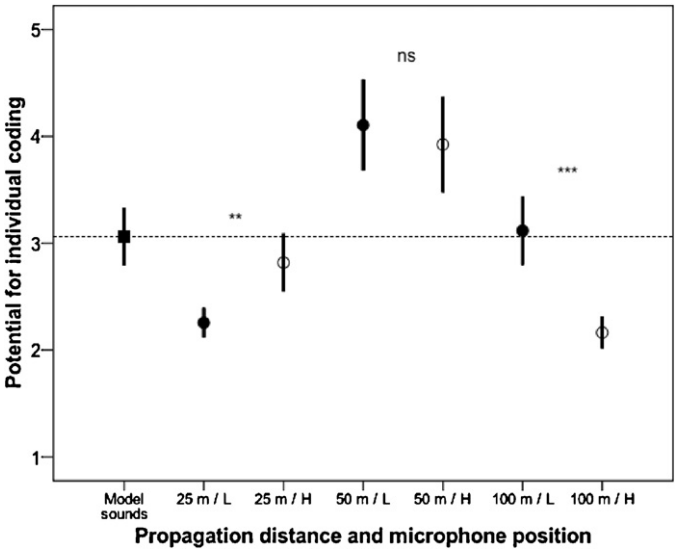

Fig. 4. Comparison of the potential of individual coding expressed as CV_b/mean CV_i ratios of 15 PPD measurements (means ± s.e.) for model sounds and propagated sounds recorded at various distances (25, 50, 100 m) and for when the microphone was placed at 25 cm (L) and 250 cm (H) above the ground. Paired t-tests for propagated sounds at three distances and different microphone heights: $^{**}p < 0.01$, $^{***}p < 0.001$, ns – non-significant.

After 100 m of transmission the potential of coding identity was significantly higher for sounds recorded close to the ground in comparison to those recorded at 250 cm ($t = 4.683$, $p < 0.001$; Fig. 4). The mixed-effect regression revealed no significant effect for distance ($z = 0.58$, $p = 0.56$) and height of the microphone ($z = -0.30$, $p = 0.761$) on the duration of PPD. Hence, clearly time between following pulses within calls remained practically unchanged after propagation regardless of the distance and position of microphone.

4. Discussion

Our results support earlier findings that PPD structure contains information about male identity (May, 1998; Peake et al., 1998). Moreover we demonstrated that the temporal structure of PPD remains practically constant after 100 m of propagation through dense vegetation. As the PPD structure preserves it's potential for individual coding after a long-distance propagation, it appears a good candidate for an individual recognition cue used by corncrakes during nocturnal territorial activity. Corncrakes are vocally active at night and in dense vegetation they have a limited possibility of seeing rivals. As a consequence, their territorial defence relies only on acoustic signals. To interact efficiently birds have to be able to localize and recognize their rivals (Naguib and Wiley, 2001). Only then can an appropriate decision on the strength of response be made. An earlier study on the variation in the amplitude spectra of corncrake calls suggested that it evolved under strong selection pressure from the potential for localization (Osiejuk and Olech, 2004). Thus it seems that the corncrake call enables precise localization as well as individual recognition of signallers during territorial interactions which are deprived of visual cues. Thus it is rather not surprising that the corncrake call acoustic characteristics is so different even in comparison to a closely related African crake *Crex egregia*. The African crakes prefer similar habitat and both species coexist during the corncrake wintering, but the African crake is active (including calling activity) during morning and evening hours (Taylor, 1985). It is worth remembering that despite corncrake males possessing territorial behaviour, i.e. they defend some resources and are aggressive towards other males, their territoriality is quite specific.

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Males may aggregate in a way resembling lekking behaviour and sometimes they swap 'territories' night after night. However, in contrast to a typical lek, both males and females do not have opportunity to see each other even from a very short distance. In addition, changing calling places after a first breeding attempt is also typical (Cramp and Simmons, 1980; Green et al., 1997, personal observations). Therefore, both good acoustic ranging and recognition tools seem to be essential for this species.

Although it is unlikely that corncrakes communicate over vegetation, placing control microphones at 250 cm allowed for a comparison between PPD transmitted through and PPD transmitted over dense vegetation. Our experiment revealed that corncrake calls propagate better (by meaning of changes in PPD structure) through the vegetation than over the vegetation. The 'acoustical design' of the corncrake call is very well adapted for transmission through dense vegetation and close to the ground. It is worth mentioning that at the same time the call structure understood as acoustic energy distribution in frequency domain, is heavily degraded due to propagation. Corncrakes are predominantly terrestrial and therefore they cannot optimize transmission or reception of their signals by changing their position vertically (Dabelsteen et al., 1993). However, it seems that the PPD structure is very resistant to degradation induced by vegetation and it seems that it is more stable at longer transmission distances when it travels through a dense environment than through the air. This could be an effect of light wind blowing over the vegetation, which may potentially affect PPD structure more than reflections from plant objects for sound propagated through vegetation. However, there was no wind during our experiment. The lack of wind gives us reason to suppose that the vegetation may act as a filter for the pulsating signal. The vegetation filter sufficiently removed the softer part of calls (i.e. gaps between pulses) while the energy peaks of loud pulses remain. Not only do they remain but, what is more important they remain with unchanged time between following peaks, as in open grassland the effect of reverberation could be ignored (Bradbury and Vehrencamp, 1998; Brumm and Naguib, 2009). As a result, the time differences between the following pulses within a call could be easier to detect after transmission through vegetation than over vegetation. Detection over vegetation could be changed, at least potentially, by a wind and temperature gradient which may likely affect sound in time domain. Simultaneously, as the typical corncrake habitats are marshes, the negative influence of the ground effect is likely to be of minor importance (Cosens and Falls, 1984).

It is also interesting that, despite a very loud call (hearing range up to 1–1.5 km, Schäffer and Koffijberg, 2004), males respond to playback only in relatively short distances of less than 50–100 m (Ręk and Osiejuk, 2010). Thus, the high call amplitude likely resulted from broadcasting calls also to females, which may hear many males at a time. The females have to choose among them (at least at the first stage) based on acoustic cue. Our experiment also suggests an alternative (but not exclusive) explanation. There is no doubt that overall call amplitude decreases with distance, mostly due to global attenuation and medium absorption (Bradbury and Vehrencamp, 1998). We found that timing of pulses within corncrake calls is relatively resistant to the propagation effect, but it is possible to measure (and likely perceive too) PPD over great distances only because the calls were very loud at the source. Thus, the high call amplitude of a corncrake call may also be explained by the need to be individually recognizable at relatively shorter distances than the need to maintain a range of call audibility. Despite many obvious differences, the acoustic communication of corncrakes is analogous to 'cocktail-party effect' found in penguin colonies (Aubin and Jouventin, 1998). Also here signalizing is seriously hampered (no visual signals available, dense vegetation, loudly calling conspecifics) and the correct recognition of individuals is crucial for subsequent decisions (e.g. to attack or to retreat, Ręk and Osiejuk, 2010).

To sum up, it seems that the corncrake with its pulse repetition call is an ideal model system for studying communication networks that rely solely on sound transmission. The corncrake is also ideal when it comes to studying communication networks where individual identity could be easily monitored by checking the call structure (Terry and McGregor, 2002).

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