



Habitat complexity and the structure of vocalizations: a test of the acoustic adaptation hypothesis in three rail species (Rallidae)

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The acoustic adaptation hypothesis is based on the assumption that senders are directionally selected to maximize transmission and minimize degradation; however, the two aims are not necessarily convergent. In complex habitats, where more effects that might potentially cause attenuation and degradation co-occur and longer transmission must incur a higher cost, signals should attenuate faster and have shorter transmission ranges. At the same time, such signals should be more resistant to degradation in order to preserve their communicatory function. Based on a sound transmission experiment, we tested the evidence for these predictions using territorial calls of three sympatric species of rails, inhabiting habitats with increasing complexity: Corncrake *Crex crex*, Spotted Crake *Porzana porzana* and Water Rail *Rallus aquaticus*. In the experiment, the calls were broadcasted with similar amplitudes through a heterogeneous habitat inhabited by all three species and rerecorded at different distances up to 320 m. Despite standardized amplitudes and habitats, calls of the species living in simpler habitats had longer transmission ranges but were more susceptible to degradation than calls of the species living in more complex habitats. Our results suggest that narrow frequency bandwidth is an adaptation of species inhabiting complex habitats that helps their calls to degrade less at the cost of stronger attenuation and shorter transmission range. By contrast, wide frequency bandwidth extends the range but increases degradation and thus it is used only by species inhabiting structurally simpler habitats. This study shows that, in more complex habitats, the clarity of the message is preserved at the cost of range.

Keywords: Rallidae, transmission experiment, sound degradation, sound attenuation.

The structure of acoustic signals is an outcome of long-term interactions among multiple selective factors: phylogenetic, functional, cultural and ecological. Phylogenetic constraints generate impassable frames for the signal variability (ten Cate 2004). Hence, bigger species tend to produce lower pitched songs (Ryan & Brenowitz 1985) and only species with a more elaborate muscle activity of the vocal apparatus can produce larger repertoires of vocalizations (Suthers & Zollinger 2004). Functional adaptations facilitate information transfer between senders and receivers (Morton 2000), so the sound amplitude matches the dimensions of

the spatial requirements in many species (Calder 1990), and the acoustic structure of sounds sometimes hinders eavesdropping by unintended receivers (Dabelsteen 2005). Some signal features such as dialects may evolve through cultural transmission (Janik & Slater 2003), which is a large source of variation in signal designs, but limited to only some vocal learning groups. Finally, habitat structure is a universal source of selection pressures on sound signals, creating mediums for acoustic transmission and being a source of physical rules that provide signals with their basic forms (Wiley & Richards 1978, 1982).

Sounds propagating through an environment undergo degradation and attenuation, both having important consequences for the 'active space'

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of acoustic signals (Dabelsteen *et al.* 1993, Boncoraglio & Saino 2007). Degradation refers to changes in the spectral, temporal and structural characteristics of signals during transmission, and attenuation refers to the progressive loss of signal energy with increasing distance from the source. The two terms are interrelated but degradation refers mainly to changes in signal quality and recognition, whereas attenuation is important mainly for signal detection. Sounds attenuate through spherical spreading at 6 dB per doubling of the distance between sound source and sound receiver but the attenuation may increase more as a result of atmospheric and vegetational absorption (Michelsen 1978).

Sounds degrade mainly because different frequencies attenuate at different rates and because of reverberations that affect the temporal structure of sounds. Shorter wavelengths are affected by smaller obstacles during transmission than longer wavelengths, but longer wavelengths are more sensitive to attenuation from the ground, especially if produced near the ground (Wiley & Richards 1978, 1982, Cosens & Falls 1984). As a consequence, sound attenuation and degradation are both frequency-dependent and habitat-dependent processes: lower frequencies transmit more easily through vegetation than higher frequencies, but higher frequencies are less sensitive to ground effects.

The role of habitat structure in the evolution of properties of acoustic signals forms the essence of the acoustic adaptation hypothesis (AAH) (Morton 1975). According to the AAH, habitats with complex vegetation favour the transmission of vocalizations with low frequencies, narrow bandwidths and low frequency modulations, while open grasslands favour the transmission of vocalizations with high frequencies, broad bandwidths and high frequency modulations (Morton 1975). The AAH is based on the assumption that senders are directionally selected to maximize transmission and minimize song degradation (Endler 1992); however, the two aims are not necessarily convergent. The fact that animal vocalizations become adapted to the acoustic properties of the habitat does not necessarily imply the maximization of transmission distances. Indeed, a number of studies have already demonstrated that birds do not maximize the active space of their vocalizations but that acoustic parameters, such as amplitude, are individually adjusted based on social context and environmental conditions

(reviewed in Catchpole & Slater 2008). Nevertheless, even when controlling for the amplitude, signals may still attenuate and degrade at different rates (Ręk 2013b). In more complex habitats, where more effects that might potentially cause attenuation and degradation co-occur and longer transmission must incur higher energetic cost, signals should attenuate faster and have shorter transmission ranges. By contrast, such signals should be more resistant to degradation in order to preserve their communicatory function. Therefore, we should expect that signals of species inhabiting complex conditions should have shorter transmission ranges and be more resistant to degradation than signals of species inhabiting simpler conditions if transmitted with similar amplitudes and in standardized conditions.

Based on a sound transmission experiment, this study aimed to test the evidence for both predictions of the AAH. In optimal conditions, the transmission range and pattern of signal degradation are characteristic for a given species and signal. However, signals are more likely to propagate through heterogeneous habitats consisting of a mosaic of optimal and suboptimal areas, and song degradation may increase or decrease when transmission occurs in habitats different from the original one (Gish & Morton 1981, Nemeth *et al.* 2001). In suboptimal conditions, vocalizations of different species change differently because different acoustic structures have different optimal conditions for transmission. For example, forest is a more restrictive habitat for sound propagation than grassland because tree-covered areas contain more barriers to sound propagation (Slabbekoorn *et al.* 2002). Consequently, broad-band calls optimal for a herbaceous habitat and propagated through a forested area will degrade more than narrow-band calls optimal for a forested area and propagated through a herbaceous habitat. Therefore, for the predictions of the AAH to be valid, signals of species inhabiting more restrictive conditions should attenuate faster and reach shorter ranges than signals of species inhabiting less restrictive conditions, if both are played in intermediate conditions. At the same time, if played in intermediate conditions, signals of species inhabiting less restrictive conditions should degrade more than signals of species inhabiting more restrictive conditions.

In this study, we used territorial broadcast calls of three sympatric species of rails (Rallidae): Corn-crake *Crex crex*, Spotted Crake *Porzana porzana*

and Water Rail *Rallus aquaticus*. Territorial calls of rails are suitable models for studying the evolution of acoustic communication because they are simple, loud tonal sounds, produced in long series. Also, they are genetically coded, which eliminates the confounding effect of cultural transmission (but see Ręk 2013a). The chosen species are characterized by similar spatial distributions and equally simple communication systems (Cramp & Simmons 1980); however, they prefer habitats with increasing complexity. Corncrakes prefer dry grasslands, Spotted Crakes prefer marshes with swampy ground or shallow water, and Water Rails inhabit wetlands with higher and diversified vegetation and a permanently submerged surface. Corncrake calls are broad-band repeated pulse signals and Water Rail calls are narrow-band signals with small modulation; the bandwidth and level of modulation of Spotted Crake calls are intermediate (Fig. 1). Despite similar amplitudes (80–100 dB sound pressure level (SPL) at 1 m in all species; see Methods section for more details), calls of Water Rail can be heard usually from perceptibly shorter distance than calls of Corncrakes and Spotted Crakes, but it is unknown whether this difference is an effect of the habitat or the acoustic structure of Water Rail calls. The predictions of the AAH would be confirmed by Water Rail calls having the highest attenuation and lowest degradation, Spotted Crake calls having intermediate attenuation and degradation, and Corncrake calls having the lowest attenuation and the highest degradation when played under standardized conditions.

METHODS

Study site and species

The propagation experiment was conducted in the Kampinoski National Park (KPN) (central Poland, 52.31617°N, 20.35560°E) on 20/21 May 2014, between 2200 and 2400 h local time. The central part of KPN provides a natural laboratory for studying the ecology of rail vocalizations. The area consists of a mosaic of dry and wet meadows, marshes, open water, dense thickets and alder groves. Because of the high heterogeneity of the environment, the habitats of sympatric rail species are distributed irregularly and unpredictably. Consequently, vocalizations between territories of conspecifics cross habitats of heterospecifics that are

more or less penetrable for sound and intermediate terrain that has the characteristics of optimal and suboptimal habitats for all species. The microphones were located in a patchy terrain dominated by grasses, sedges (*Carex gracilis* and *Carex acutiformis*), Common Reed *Phragmites australis*, Common Bulrush *Typha latifolia* and willows *Salix* spp. In 2014, this area was inhabited by Corncrakes, Spotted Crakes and Water Rails, with Corncrakes preferring vegetation patches dominated by grasses and sedges, Spotted Crakes preferring partially flooded marshes and Water Rails inhabiting reed beds with open water. Nevertheless, the fact that all three species can be found in different areas of the park with higher densities suggests that the study area was not the preferred habitat of any species. Weather conditions and ambient background noise remained similar throughout the experiment (temperature, 14–17 °C; noise (SPL), 43–47 dB(A)).

Corncrakes, Spotted Crakes and Water Rails are small to medium-sized rails (27–30, 22–24 and 23–28(30) cm in length, respectively) (Taylor 1998). Corncrakes are polygynous, whereas Spotted Crakes and Water Rails are monogamous. In Poland, Spotted Crakes and Water Rails start to call about a month earlier (mid-April) than Corncrakes but all three species call with two distinct peaks of vocal activity (Schäffer 1999, Osiejuk *et al.* 2004, Polak 2005). All three species have repertoires of several call types, some of which are very quiet and produced mostly during aggressive interactions (Cramp & Simmons 1980, Ręk & Osiejuk 2011b, Ręk 2015). Others are very loud and function as territorial signals and individual fingerprints (Ręk & Osiejuk 2011a, Budka & Osiejuk 2013, Ręk 2015). Such loud calls are common among rails, but differ markedly even among closely related taxa (Taylor 1998). Furthermore, the calls are produced in specific temporal patterns, which have been suggested to transfer information about aggressive motivation of the signaller independently from the calls themselves (Ręk & Osiejuk 2013, Ręk 2015). Such patterns differ among species no less than the calls themselves. In Water Rails, the calls are produced in accelerating and decelerating series but the function of such patterns has not been studied. In Corncrakes there are two rhythmic variants, monotonous and intermittent, which encode submissive or passive and aggressive motivation, respectively (Ręk & Osiejuk 2010). The organization of Spotted Crake calls is

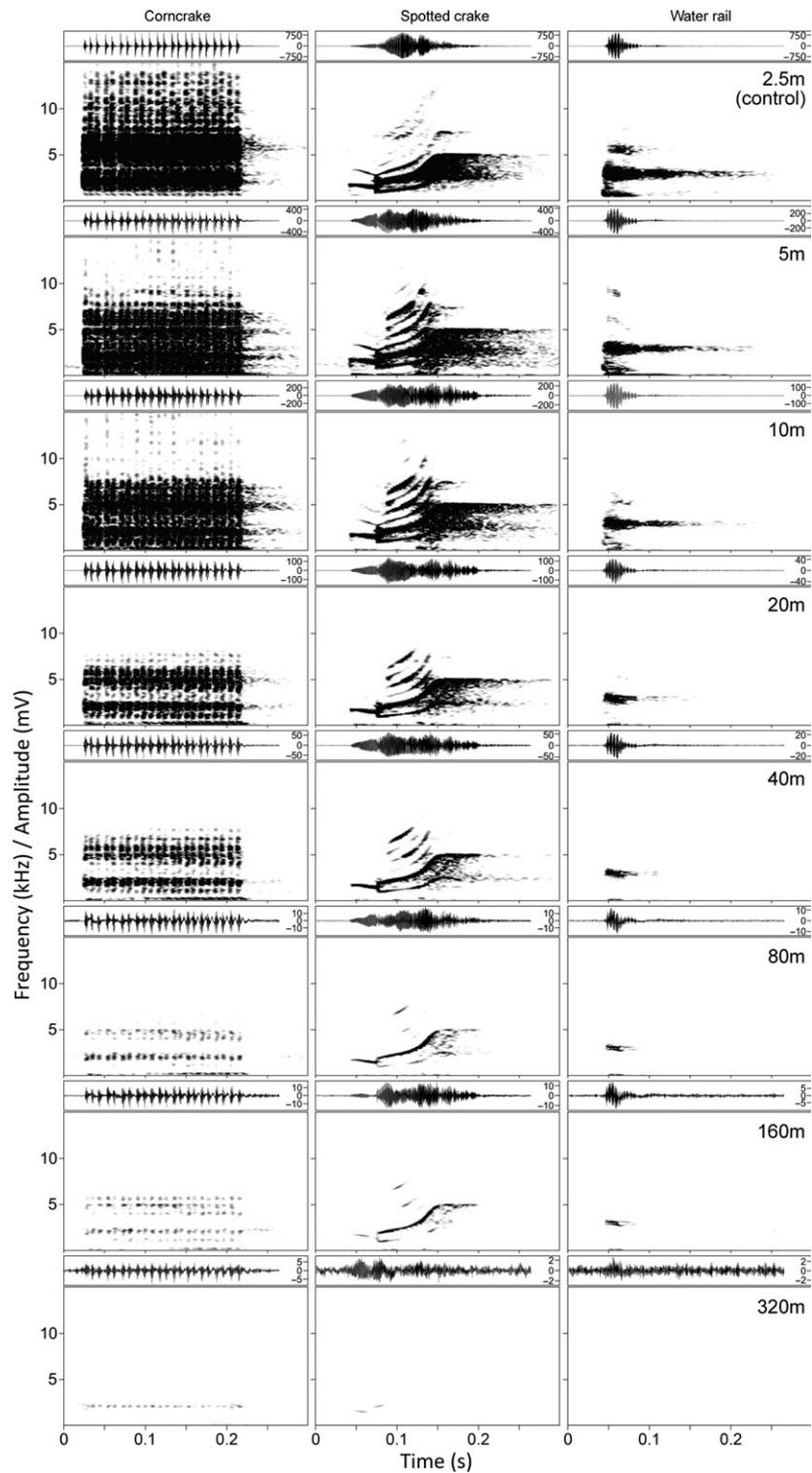


Figure 1. Sonograms of Corncrake, Spotted Crane and Water Rail control and propagated calls. Sonograms come from three calls played once and rerecorded at different distances after propagation. Recordings used to generate these sonograms are available as Supporting Information.

harder to define but the length of intervals between calls was linked to the aggressive motivation of males (Ręk 2015). We know little about the mechanisms of vocal production in these species. The loudest territorial calls are uttered with heads pointed upwards, which probably maximizes their amplitude (personal observation).

Transmission experiment

To assess the modifications of signals of sympatric species during propagation through the heterogeneous habitat, the calls of each species were broadcasted repeatedly and recorded at seven different distances during one night. Because all microphones recorded simultaneously, all calls were recorded by all microphones. The microphones were located in randomly selected directions within an angle of 2° along a more or less east–west diagonal. This meant that sounds propagating between the speaker and microphones crossed similar but not the same vegetation. We recognize that the patterns generated by the distance might be confounded with the structure of vegetation. However, we think this is unlikely given the spatial range of the experiment and the high level of spatial heterogeneity of the vegetation.

Test sounds

We used 244 samples of Corncrake calls recorded from 16 males (8–20 per male), 275 samples of Spotted Crake calls recorded from 15 males (15–20 per male) and 59 samples of Water Rail calls recorded from three males (19–20 per male). Calls were recorded in the same area in 2008–13 with Edirol R9 (Roland Corp., Hamamatsu, Japan) (frequency response: 20–22 000 Hz) or Marantz PMD620 (Marantz, Kanagawa, Japan) (frequency response: 20–22 000 Hz) portable recorders and Sennheiser ME 67 (Sennheiser electronic GmbH & Co. KG, Wedemark, Germany) microphones (frequency response: 40–20 000 Hz, ± 2.5 dB) with windscreens, and all recordings were within 3 m of the calling bird. Calls were digitized using the AVISOFT SASLAB PRO 5.2 (Avisoft Bioacoustics, Glienicke, Germany) sound analysis package (44.1-kHz/16-bit pulse code modulation (PCM) files). Calls from each male were saved and later played back at their natural rates (i.e. in natural series) and there were pauses a few seconds long between calls of consecutive

males to allow for the analysis of the background noise. The peak amplitude of each playback sample was prepared to match 90 ± 3 dB(A) (SPL at 1 m), which is within the natural levels of territorial calls of all three species, and the distributions of SPL were similar among species. This value was a good approximation of natural peak amplitudes for all species: 91.45 dB(A) (SPL at 1 m) for the Corncrake, 91 dB(A) for the Spotted Crake and 90.25 dB(A) for the Water Rail, which were measured by the authors (P. Ręk & K. Kwiatkowska pers. obs.) from 10 males, seven males and four males, respectively. The SPL values were measured with a UT352-Sinometer SPL meter (Sinometer Instruments, Shenzhen, China) from 10 calls of each individual, and only when the male's head was directed towards the level meter. These measurements were taken within 3 m of the calling birds and standardized to 1 m based on the inverse square law.

Experimental set-up and field recording

The seven microphones for rerecording of the tested signals were placed at 5, 10, 20, 40, 80, 160 and 320 m from the speaker, each in a different direction from the speaker. Calls recorded with these seven microphones are referred to as propagated sounds. Additionally, all test sounds were recorded in an open quiet area at 2.5 m from the speaker to prepare control sounds to be compared with the propagated sounds during the calculation of response measures (see the section 'Sound analysis and response measures' below for details). The control and propagated sounds were recorded simultaneously, which meant that each call played was rerecorded eight times; however, the area between the speaker and the control microphone was cleared of vegetation to minimize degradation of control recordings. Furthermore, in a preliminary trial, we tested one extra microphone placed at 640 m in order to cover the whole range of propagated sounds; however, either the quality of calls recorded was very poor or the calls were indistinguishable from the background noise. Therefore, we believe that a 320-m range enabled us to estimate a high proportion of the range of transmission causing changes of the tested sounds. Both the speaker and the microphones were placed *c.* 50 cm above ground level; however, this height was measured from the solid ground rather than from the surface of the vegetation on which

birds usually stand. Such a height was assumed to reflect the natural position of studied birds that call and listen with bodies elongated and with heads directed upwards (P. Reĳ & K. Kwiatkowska pers. obs.). Signals were emitted by a Creative ZEN (Creative Technology Ltd., Jurong East, Singapore) player (quality of files: PCM, 48 000 Hz, 16 bits) connected to a MIPRO MA 101 (Mipro, Chiayi, Taiwan) loudspeaker with a 45-W amplifier (frequency range 60–15 000 Hz and linear frequency response within species-specific frequency range).

Recordings of propagated and control sounds were made with a wireless custom-designed system. The system consisted of eight omnidirectional Sennheiser ME 62 microphones (frequency response: 150–15 000 Hz, ± 2 dB) connected to eight Sennheiser SKP3000 transmitters, two passive directional antennas (Sennheiser A 2003 UHF), eight Sennheiser EK 3241 receivers housed in two synchronized racks (Sennheiser QP 3041), and an RME Multiface II multichannel audio interface (Audio AG, Haimhausen, Germany) transmitting digital signal to a Lenovo ThinkPad W530 (Lenovo Group Ltd., Beijing, China) laptop. Thanks to this system, we avoided strong resistance of cables and could visually control the recording process in real time. The problem with the use of cables in transmission experiments is that each microphone in the system should be connected to the receiver with a cable of the same length and type; otherwise, proper calibration of the recording system can be impossible. Such an approach limits considerably the spatial range of transmission experiments and the number of microphones used, but it cannot be fully compensated for with the calibration of the amplitude. Nevertheless, this problem has not been raised in previous studies, whose methods usually do not contain details regarding the calibration of recording systems.

Calls were played back and rerecorded with short breaks for 2 h so that we had multiple recordings of each sample; however, only one version of each sample was used in further analyses. Because the same calls were recorded from multiple microphones simultaneously, we first selected calls with similar quality in all channels considering the distance to the microphones. If more than one version of a given sample was obtained, the final selection was random. For digitization and monitoring we used the AVISOFT RECORDER 4.2 (Avisoft

Bioacoustics) software (44.1-kHz/16-bit PCM multichannel files). Prior to the experiment, this system was checked for any systematic variation in the amplitude and spectral structure of calls between the radio microphones located at different distances from the receiving antennas. However, we did not find any systematic variation in the amplitude or structure of calls within the range we used; the recording box was placed in the middle of the study site, so that the distance to the furthest microphone did not exceed 200 m. Also, to maximize the range of the system, radio-transmitters were not attached directly to the microphones but connected with 2-m-long cables and placed at the top of the stick, and antennas were hung on trees a few metres above the ground.

Sound analysis and response measures

Degradation was estimated by comparing the propagated sounds with control sounds using the program SIGPRO v3.23 (Pedersen 1998) and an established protocol (Dabelsteen *et al.* 1993, Holland *et al.* 1998, 2001, Balsby *et al.* 2003). The tested sounds were not masked by transient noise, and the pause after the sound should only contain the echo of the sound and the stationary background noise. For each sound, the background noise energy (E_{noise}) was estimated from a 1-s pause, which did not contain transient sounds. The propagated sounds were all compared with their respective control sounds. All three sound types propagated as well as control sounds, and the background noise within their respective frequency ranges was individually band-pass filtered using high- and low-pass values deduced from visually inspecting the spectrogram. The propagated and control sounds were aligned in time by maximizing the cross-correlation function between them. The matching allowed determination of the precise position of the propagated signal on the time axis and thus quantification of the energy (E_y) in the propagated sound within the time-frame of the control sound. The signal-to-noise ratio was calculated as $\text{SNR} = 10 \log ((E_y - E_{\text{noise}})/E_{\text{noise}})$ (Dabelsteen *et al.* 1993, Balsby *et al.* 2003).

The matching of the waveform of the observation sound with that of the control sound was also used for calculating the excess attenuation (EA). The EA describes the amount of attenuation of

the sound that cannot be attributed to attenuation by spherical spreading Attenuation (A) = 6 dB per doubling of distance), and it was calculated as $EA = -20 \log(k) - A$. After alignment of the functions, the ratio (k) between the observation waveform and the control waveform was determined. Usually, it is the amplitude function that is matched to calculate the k ratio (Holland *et al.* 1998), but k based on the waveform may be used in cases where it is meaningless to compare envelope functions, for example when signals are very complex or contain strong harmonics or broadband chaotic sounds (Pedersen 1998). Because of the low amplitude and pure quality of Water Rail calls at 320 m, these recordings could not be aligned reliably with their respective control sounds. Consequently, we could not calculate SNR and EA values for the Water Rail propagated sounds at 320 m.

Given their formulas, SNR and EA are usually strongly negatively correlated. SNR provides an overall test of the net effect of masking and attenuation; it depends mainly on the spectral structure of the background noise and the level of negative interference. EA depends mainly on the spectral structure of the signal itself and it increases as a result of absorption and scattering of signal energy. Because the transmission range of the signal depends on the SNR and the rate of absorption of signal energy by the habitat, both parameters are useful in comparing transmission ranges of whole sounds; however, they are not appropriate measures of changes in spectral structures of sounds during transmission.

To evaluate changes in the spectral structure of calls within their ranges, we measured the distribution of energy across frequency spectra. We integrated and divided spectra into four equal parts, separated by the three frequencies: quartile 25% (Q25): below this frequency is 25% of the total energy; quartile 50% (Q50): the median frequency of the spectrum, below which is 50% of the total energy; and quartile 75% (Q75): below this frequency is 75% of the total energy. We used these energy quartiles to describe changes in the distribution of energy in the frequency spectrum of sounds and to locate the frequency ranges most susceptible to degradation and attenuation. Consequently, these measures were used to assess changes in the quality of calls. Energy quartiles were calculated based on sonograms generated in the AVISOFT SASLAB PRO software, excluding

recordings from 320 m, for which the signals were too blurred with the background noise to allow reliable measurements.

Data analysis

To compare the measurements of degradation among calls of three species at consecutive distances (six distances for energy quartiles or seven for SNR and EA), we used generalized estimating equations (GEEs), which can properly handle correlated or repeated measures data (Hardin & Hilbe 2002). This method was used specifically in order to control for potential non-independence among calls of the same individual and among the same calls rerecorded at consecutive distances. A Bonferroni sequential method was used in GEEs to create confidence intervals for differences between consecutive distances for a given species and among species for a given distance. To compare background noise levels, measured within filter frequency ranges specific for given sound types, we used analysis of variance (ANOVA). Because we sampled only the background noise, without the sounds played by the speaker, we treated noise measurements as independent. Furthermore, to maximize the accuracy of our estimates we measured noise in recordings from all microphones, including the control microphone, because sampling of noise does not require any control. Some sounds recorded between 5 and 320 m (20 out of 4565) that were strongly masked by sounds of animals were excluded from the analysis. All P -values are two-tailed. All statistics were calculated in SPSS v22.0 (IBM Corp., Armonk, NY, USA). If not stated otherwise, means are given ± 1 se.

RESULTS

Range

Despite similar amplitudes at which we played back call samples, calls of Corncrake, Spotted Crake and Water Rail had different ranges of transmission (Fig. 2). At 5 m, calls of Water Rail had significantly higher SNR than calls of Corncrake but by 160 m all call types had similar SNR (Fig. 2). At 320 m, a majority of Water Rail calls were undetectable from sonograms and their energy was too low relative to the noise to be correctly measured (Fig. 1). Mean background noise levels, measured within filter frequency ranges

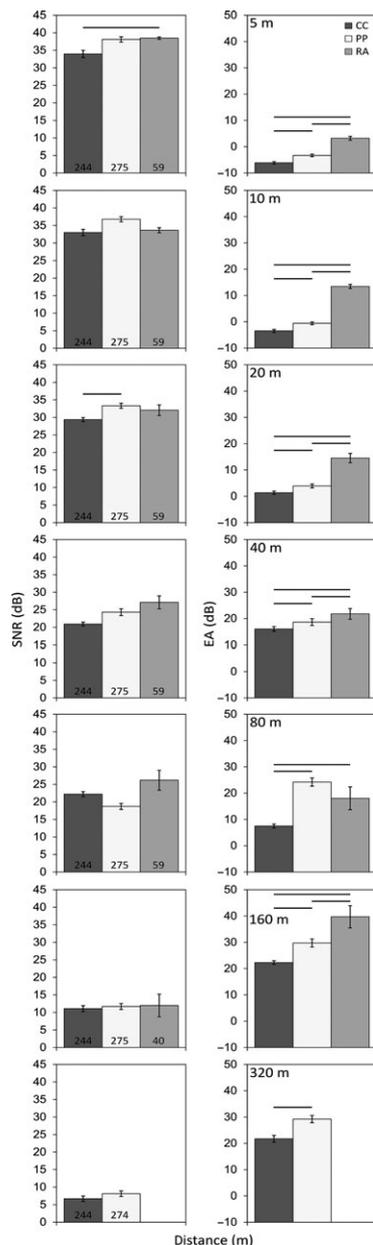


Figure 2. The distribution of signal-to-noise ratio (SNR) and excess attenuation (EA) among three species of rails, Corncrake (CC), Spotted Crane (PP) and Water Rail (RA), at seven distances. Error bars denote one standard error of the mean. Significant differences are indicated with thick black lines. Numbers on the bars denote sample sizes (the same for SNR and EA).

specific for given sound types from both propagated and control sounds, were highest for Corncrake calls and lowest for Water Rail calls (Corncrake: 26.72 ± 0.15 dB; Spotted Crane: 25.40 ± 0.14 dB; Water Rail: 19.26 ± 0.34 dB;

ANOVA: $F_{2,4542} = 199.90$, $P < 0.001$). Correspondingly, the calls differed markedly in EA at consecutive distances: Water Rail calls consistently had the highest EA, Corncrake calls had the lowest EA, and Spotted Crane calls had intermediate EA values (Fig. 2).

Quality

Even though Water Rail calls were most susceptible to excess attenuation, these calls attenuated more in their entirety because the distribution of energy among frequencies was relatively stable throughout their range (Fig. 3). Conversely, attenuation in Corncrake and Spotted Crane calls was frequency dependent (Fig. 3). Calls of Spotted Crane and Corncrake in particular underwent abrupt and significant changes in their intermediate and high frequencies, with generally opposing directions at consecutive distances (Fig. 3). While Spotted Crane calls lost more energy in higher frequencies (decreasing Q50 and Q75), Corncrake calls lost more energy in intermediate frequencies and vice versa (increasing Q50 and Q75).

DISCUSSION

Despite similar amplitudes and conditions, signals of species inhabiting less complex habitats had longer transmission ranges than signals of species inhabiting more complex habitats; however, signals of species inhabiting more complex habitats were more resistant to degradation. It appears that the narrow frequency bandwidth can be an adaptation in species inhabiting acoustically more restrictive conditions, leading to the preservation of high quality, potentially at the expense of stronger attenuation and shorter transmission range. However, a short transmission distance does not necessarily reflect a trade-off between degradation and active range, because the transmission distance could simply be adapted to territory size or typical male–male or male–female spacing, all of which may differ between species; this study points to the possibility of such a trade-off.

Acoustic structures of calls of Corncrake, Spotted Crane and Water Rail, respectively, appear to be adapted to the transmission through their increasingly complex habitats. In habitats preferred by Corncrake for calling, absorption of sound energy can be high for frequencies lower than 2 kHz because porous soil covered with decaying

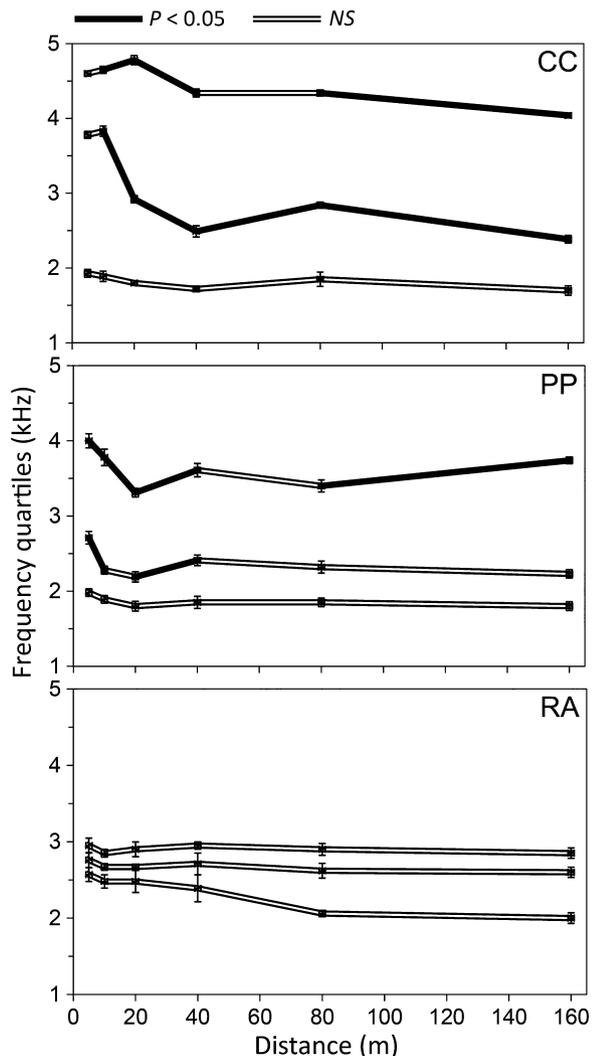


Figure 3. The distribution of energy across frequency spectra of three rail species during propagation through the heterogeneous habitat. The three lines for each species indicate quartile 25% (below this frequency is 25% of the total energy), quartile 50% (the mean frequency of the spectrum), and quartile 75% (below this frequency is 75% of the total energy). CC, Corncrake; PP, Spotted Crake; RA, Water Rail. Filled lines indicate significant differences from the preceding distance. Error bars denote one standard error of the mean. NS, not significant.

herbs is a highly absorptive medium, especially for sounds produced near the ground (Piercy *et al.* 1977). However, most of the energy in Corncrake calls can be found above 2 kHz. Also, the scattering of higher frequencies caused by surrounding objects should be negligible because Corncrake optimal habitat consists mainly of grasses. Therefore, in optimal conditions Corncrake calls propagate for

long distances and males can be heard from at least 1 km (Schäffer & Koffijberg 2004). Previous research on the Corncrake showed that its calls, with wide frequency spectrum and repeated pulse structure, are remarkably resistant to degradation in their optimal habitat (Ręk & Osiejuk 2011a, Ręk 2013b), and a similar effect has been observed for many species inhabiting grasslands (Wiley 1991). Nevertheless, Corncrake calls were degraded more than calls of Water Rail and Spotted Crake while transmitted through the partially flooded habitat with a more complex vegetation composition. Therefore, it seems likely that the wide frequency spectrum responsible for the long range of Corncrake calls in their optimal habitat is the main reason for their frequency-dependent attenuation in suboptimal conditions.

In conditions preferred by Water Rails, sound waves are subjected to strong reflections from the water surface and to filtering by dense and tall vegetation. Ground effects are particularly destructive for modulation in the time domain, but, in contrast to Corncrakes, Water Rails produce non-pulsative tonal calls. In fact, such narrow-band calls can even be amplified by reverberations (Slabbekoorn *et al.* 2002). By contrast, dense vegetation filters out higher frequencies, and the effect of tall reeds, dense thickets and scattered trees inhabited by Water Rails must be stronger than the effect of soft grasses preferred by Corncrakes. In such complex conditions, broad-band sounds degrade more than narrow-band sounds and thus narrow-band signals dominate (Boncoraglio & Saino 2007). In accordance with the predictions of the AAH, the calls of Spotted Crake and, in particular, Water Rail played back in a heterogeneous habitat did not transmit as well as Corncrake calls. Also, Water Rail calls were more resistant to frequency-dependent attenuation than Corncrake calls at intermediate and higher frequencies, and Spotted Crake calls were more resistant to attenuation of intermediate frequencies than Corncrake calls. Given similar natural amplitudes and the same playback amplitudes, these differences suggest that the different transmission ranges of calls of Corncrakes, Spotted Crakes and Water Rails resulted from their different frequency bandwidths. Conversely, these differences could not be an effect of body size because the Water Rail, the species with the shortest transmission range of calls in our experiment, is almost as big as the Corncrake and bigger than the Spotted Crake (Taylor 1998).

It has been suggested that concentrating energy within a narrow band, as opposed to spreading the same energy through a broader range of frequencies, may lead to an increase in amplitude, and consequently an increase in transmission distance despite habitat limitations (Morton 1975, Marten *et al.* 1977, Wiley & Richards 1982). Nevertheless, the assertion that tonal signals travel farther because more energy is concentrated in one bandwidth should be treated with caution because it is valid only if energy concentration is associated with an increase in amplitude. The amplitudes of the calls of the studied rails were similar, which suggests that Water Rails invest less energy in production of their narrow frequency calls to achieve similar amplitudes, and this resulted in stronger excess attenuation and shorter transmission ranges during the transmission experiment. Narrow frequency bandwidth is indeed a less sensitive design to frequency-dependent attenuation and in more complex habitats energy may need to be concentrated over small frequency bands to preserve high propagation ranges (Boncoraglio & Saino 2007). Moreover, studies comparing degradation of songs in open and complex habitats show that whistles degrade less than amplitude-modulated trills in both habitats (Brown & Handford 2000). Nevertheless, open areas are dominated by wide-frequency vocalizations and it seems that birds prefer wide bandwidths as long as higher and lower frequencies are not filtered out. This study shows that such wide-bandwidth calls have longer transmission range than narrow-bandwidth calls, in both open and complex habitats.

Contrary to many previous studies testing the degradation of calls in the species' preferred habitat, we studied the effect of the mixed habitat on calls of several species. Such an approach has many benefits. First, given the range of bird songs and calls, it seems unlikely that acoustic signals are adapted specifically to one specific type of habitat. Our approach therefore reflects more natural circumstances. Secondly, mixed habitats provide natural settings for sympatric species, in which each species has preferences for some conditions but all elements are natural and frequently experienced by all species. Mixed conditions therefore provide natural control conditions for testing the transmission properties of acoustic signals in multiple species simultaneously. If birds were tested separately, in a different habitat for each species, the results would not be comparable. Thirdly, the habitat preferred is

not necessarily the best habitat for acoustic transmission. In the study area, Corncrakes often call from depressions overgrown with tall herbaceous vegetation and surrounded by trees. Such locations are probably chosen because of their safety but sounds produced there have a short range because of extreme reverberations. Our approach also has some limitations. First, because different sound characteristics may interact differently with different areas of a mixed habitat, the standardization of conditions for all species may be unequal. However, we think that this is unlikely, mostly because of the level of heterogeneity of the studied habitat and the number of microphones used. Given that homogeneous elements of the landscape, such as patches of reeds or pools, were only a few metres long on average, the level of randomization of conditions in the experiment must have been large.

The results of this study have implications for the conservation of rails. Rails are among the animals most severely affected by human-caused changes in wetland ecosystems. In the study area, rails have been studied for more than 10 years and during this time the conditions have changed from relatively dry to very wet. Many areas inhabited a few years ago by Corncrakes are flooded now and the population of Corncrakes has decreased notably. By contrast Spotted Crakes, which were limited to some particularly wet areas, can now be heard from the the spots previously occupied by Corncrakes throughout the park. Water Rails were heard sporadically and now are regular inhabitants. The park is cut through by an artificially straightened river that for decades drained the centrally located wetlands, but because of the increasing and unregulated activity of Beavers *Castor fiber* the water flow has been radically limited. The vegetation composition does not seem to have changed much yet but the water level has increased, and this effect is reflected in changes in populations of rails. Considering the negative effect of the flooded habitat with a complex vegetation composition on the quality of Corncrake calls, this study may suggest some indirect effect of communication on species distribution and abundance in this group of very vulnerable birds, which could be reflected in conservation decisions during restoration of habitats to their natural state.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

- Audio S1.** *Crex crex* call, 2.5 m (control).
Audio S2. *Crex crex* call, 5 m.

- Audio S3.** *Crex crex* call, 10 m.
Audio S4. *Crex crex* call, 20 m.
Audio S5. *Crex crex* call, 40 m.
Audio S6. *Crex crex* call, 80 m.
Audio S7. *Crex crex* call, 160 m.
Audio S8. *Crex crex* call, 320 m.
Audio S9. *Porzana porzana* call, 2.5 m (control).
Audio S10. *Porzana porzana* call, 5 m.
Audio S11. *Porzana porzana* call, 10 m.
Audio S12. *Porzana porzana* call, 20 m.
Audio S13. *Porzana porzana* call, 40 m.
Audio S14. *Porzana porzana* call, 80 m.
Audio S15. *Porzana porzana* call, 160 m.
Audio S16. *Porzana porzana* call, 320 m.
Audio S17. *Rallus aquaticus* call, 2.5 m (control).
Audio S18. *Rallus aquaticus* call, 5 m.
Audio S19. *Rallus aquaticus* call, 10 m.
Audio S20. *Rallus aquaticus* call, 20 m.
Audio S21. *Rallus aquaticus* call, 40 m.
Audio S22. *Rallus aquaticus* call, 80 m.
Audio S23. *Rallus aquaticus* call, 160 m.
Audio S24. *Rallus aquaticus* call, 320 m.