

Do aggressive signals evolve towards higher reliability or lower costs of assessment?

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Abstract

It has been suggested that the evolution of signals must be a wasteful process for the signaller, aimed at the maximization of signal honesty. However, the reliability of communication depends not only on the costs paid by signallers but also on the costs paid by receivers during assessment, and less attention has been given to the interaction between these two types of costs during the evolution of signalling systems. A signaller and receiver may accept some level of signal dishonesty by choosing signals that are cheaper in terms of assessment but that are stabilized with less reliable mechanisms. I studied the potential trade-off between signal reliability and the costs of signal assessment in the corncrake (*Crex crex*). I found that the birds prefer signals that are less costly regarding assessment rather than more reliable. Despite the fact that the fundamental frequency of calls was a strong predictor of male size, it was ignored by receivers unless they could directly compare signal variants. My data revealed a response advantage of costly signals when comparison between calls differing with fundamental frequencies is fast and straightforward, whereas cheap signalling is preferred in natural conditions. These data might improve our understanding of the influence of receivers on signal design because they support the hypothesis that fully honest signalling systems may be prone to dishonesty based on the effects of receiver costs and be replaced by signals that are cheaper in production and reception but more susceptible to cheating.

Introduction

The evolution of animal communication is a consequence of the costs and benefits associated with signalling by senders and responding by receivers (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; Vehrencamp, 2000; Dawkins & Guilford, 1991; Hughes *et al.*, 2012). Because senders initiate the process of communication, the expected benefits must first outweigh all of the costs associated with signalling, with the benefits coming from the receiver's behaviour. Conversely, receivers should also benefit from assessing and responding to signals (Maynard Smith & Harper, 2003), and signals must be reliable on average to be beneficial

for receivers (Searcy & Nowicki, 2005; Seyfarth *et al.*, 2010). Nevertheless, signallers are not always selected to signal reliably. Hence, what keeps signals reliable?

Many mechanisms for maintaining signal honesty have been proposed (reviewed in: Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; Számadó, 2010; Vehrencamp, 2000). Such a state can be met readily when the interests of the two sides overlap because if signal honesty is guaranteed by the common interest, it can be advantageous for both sides to produce honest signals (Maynard Smith, 1991). Consequently, both sides can benefit from communication, even if the expected benefits are small. Nevertheless, communication most commonly occurs between conflicted, genetically distinct individuals. The problem with reliable signalling between opponents is that it requires a fitness cost balancing the potential benefits from cheating because of the susceptibility of signals to deception

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(Zahavi, 1975; Grafen, 1990; Enquist, 1985). Two general groups of such costs have been postulated: receiver-independent and receiver-dependent costs. The first group includes costs that are inherent in the form of the signal and hence stabilize their reliability irrespective of the receiver's behaviour (Guilford & Dawkins, 1995; Vehrencamp, 2000), whereas the second group includes costs that arise from the receiver's response to a signal (Enquist, 1985; Adams & Mesterton-Gibbons, 1995). The most effective forms of signals for senders and the most reliable forms for receivers are usually those that are either challenging to perform or those that are made honest by a mix of developmental and production costs, that is those that are associated with an inherent cost (Polnaszek & Stephens, 2014; Searcy & Nowicki, 2005; Møller *et al.*, 1998). However, the choice of one form of the signal instead of another appears to depend on the value of the resource involved.

Depending on the value of the contested resource, the evolution of signalling should proceed in different directions (Vehrencamp, 2000; Gil & Gahr, 2002; Maynard Smith & Harper, 2003; Hurd & Enquist, 2005). If the expected benefits (e.g. a receptive female, territory) are high, signallers should be willing to pay high physical costs to affect receivers' behaviour. Such signals should be reliable predictors of an individual's quality because opponents would have much to gain from signalling reliably and much to lose by cheating (Searcy & Nowicki, 2005; Fitch & Hauser, 2003). In the opposite situation, that is, when the expected net benefits are minimal, signals should be cheap to produce and show a more or less arbitrary form (Tibbetts, 2008). Such signals should be honest on average because senders have little to gain by cheating and receivers have little to lose by ignoring signals. At the same time, cheating would be kept at a low level through occasional evaluation by receivers and retaliation (Bywater & Wilson, 2012; Rohwer, 1975). Between these two extremes, there is a whole sphere of situations in which the expected net benefits are intermediate, and such systems appear to be the most susceptible to cheating. In these

circumstances, signals might require a combination of inherent and receiver-dependent costs to maintain their honesty (Guilford & Dawkins, 1995), or a receiver might accept some level of signal dishonesty by choosing signals that are cheaper regarding assessment but that are stabilized with a less secure receiver-dependent mechanism of reliability maintenance (Dawkins & Guilford, 1991).

Compared with the costs paid either by signallers or by receivers, less attention has been given to the effect of the interaction between these two types of costs on the reliability of signalling systems (Bywater & Wilson, 2012). Generally, signals that require more precise and time-consuming assessment tend to be more costly to produce (Clutton-Brock & Albon, 1979), although this relationship does not necessarily hold in the opposite direction (Dawkins & Guilford, 1991). Some signals may be easy to assess and costly to produce (e.g. large antlers), but if signalling involves an investment regarding the time of production or complexity, then the cost of signal assessment by receivers increases with the cost of signal production by signallers. Consequently, for many signals that are costly for signallers (e.g. the length of a male's song and the size of syllable repertoire), there may be a very narrow margin, if any, for forms of signals that can combine high reliability with a low cost of assessment, and such systems should evolve either towards lower costs of assessment or higher reliability.

The main goal of this study was to experimentally test how receivers optimize the benefits and costs of signal assessment. Would birds prefer to respond to signals that are easy to assess (minimal cost hypothesis) or signals that are more honest (maximal reliability hypothesis)? The soft calls of the corncrake (*Crex crex*) provide a good model for studying the mechanisms maintaining signal honesty during territorial conflicts. These calls are quiet, low-frequency signals consisting of two notes: an initial, very quiet, amplitude-modulated gurgling note and a final, a slightly louder and less-modulated mewling note (Fig. 1). It has been shown that the reliability of this signal is maintained by a receiver retaliation rule, rather than by inherent costs

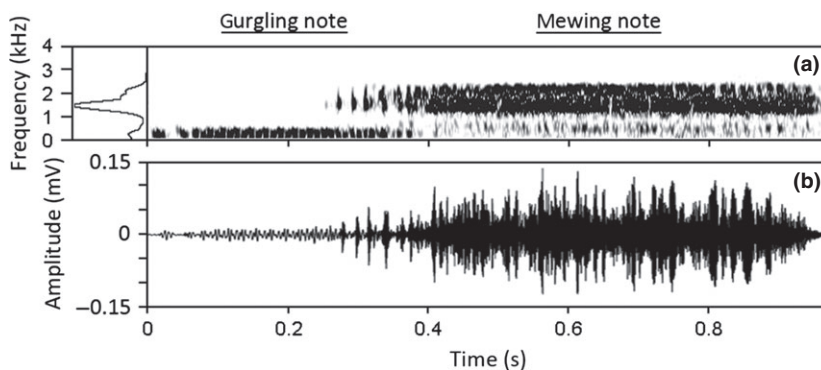


Fig. 1 Sonogram (a) and time domain waveform (b) of the corncrake's soft call. Soft calls are quiet (approximately 70 dB (a) SPL at 1 m), low-frequency signals consisting of two notes: an initial, very quiet, amplitude-modulated gurgling note (~ 0.13 – 0.6 kHz) and a final, slightly louder and less-modulated mewling note (~ 0.38 – 2.84 kHz).

(Ręk & Osiejuk, 2011), which means that it can be beneficial for receivers to respond to soft calls indiscriminately, that is, regardless of their acoustic structure. Nevertheless, the frequency spectrum of gurgling notes limits their range (Ręk, 2013), most likely because it is physically difficult or costly for a small bird to produce low-frequency sounds with a high amplitude (Fletcher, 2007), which suggests that the structure of soft calls may encode some extra information, with reliability being maintained by an inherent cost. Such physical associations have been shown to provide important information for receivers in sexual contexts (Vannoni & McElligott, 2008; Wagner, 1989). It is therefore possible that soft calling in the corncrake is associated with a combination of inherent and receiver-dependent costs, confirming the maximal reliability hypothesis. Nevertheless, the low amplitude makes the frequency spectra of gurgling notes costly to assess by receivers because receivers must make an extra effort to decode the signal well. Receivers might therefore ignore the frequency and occasionally test senders for cheating, even if the frequency is a good predictor of male quality. This option would confirm the minimal cost hypothesis.

To distinguish between these two hypotheses, it is necessary to analyse the natural variability in the frequency of gurgling notes and to test for differential responses to this variability, controlling for the cost receivers pay in assessment. This investigation was carried out in three steps: (i) analysis of the predictive value of the fundamental frequency of gurgling notes, (ii) testing of the responses of receivers to the natural variability in the fundamental frequency of gurgling notes and (iii) testing of the responses of receivers to variability in the fundamental frequency of gurgling notes while decreasing the costs of assessment paid by receivers. Correlation between the acoustic and morphological parameters is necessary to demonstrate their predictive relationship (i), although it does not imply the adaptive, signalling nature of the acoustic parameter. Additionally, it is necessary to demonstrate the differential responses of receivers to the acoustic parameter (ii). Nevertheless, playback stimulation might not trigger the differential response under typical conditions but only if the costs receivers pay during assessment are experimentally decreased (iii) or the value of information increased, indicating that an acoustic parameter is functional (is a signal) only if the costs receivers pay in assessment are low. Implicit in this argument is the assumption that under natural conditions, the cost of true assessment is not justified by what could be gained from uncovering a cheat. Positive results from the first and second steps would confirm the maximal reliability hypothesis, whereas positive results from the first and third steps and a negative result from the second step would confirm the minimal cost hypothesis.

Materials and methods

Study site and species

The data analysed in this study came from three study plots located in Poland. All of the plots and the sites of sample recording are within the continuous range of this species, and it was shown that males might cover distances similar to those among the plots even within the breeding season, due to disturbance or in search of females (Mikkelsen *et al.*, 2013). Also, it was revealed that within-population variation in corncrake calls may occur on the same scale as between-population variation (Budka *et al.*, 2014). (i) Morphometric measurements of males and the corresponding data on the acoustic parameters of soft calls were collected in Kampinoski National Park (centre of the area: 20°23 'E i 52°19 'N; ca. 80 km²) from 19 May to 12 June 2010, between 2200 and 0215 h local time, which corresponds to the peak of nocturnal vocal activity of corncrakes, in a sample of $N = 18$ males. The first playback experiment (Experiment 1) was carried out in Biebrza National Park, its surroundings and areas southward from the park (centre of the study area: 53°37 'N, 22°68 'E; ca. 1500 km²) from 17 May to 2 June 2009, between 2200 and 0215 h local time, in a sample of $N = 34$ territorial males. (iii) The second playback experiment (Experiment 2) was conducted in the Upper Nurzec River Valley in Northeast Poland (centre of the study area: 23°28 'E and 52°58 'N; ca. 40 km²) from 21 to 30 May 2013, between 2200 and 0200 h local time. The test subjects in this experiment were $N = 44$ territorial corncrake males. All fieldwork was conducted during the time of territory establishment by males, which is when males call most intensively, to attract females. Subjects were randomly selected from larger groups.

Data collection and preparation of call samples

To perform a comparative morphometric bioacoustic analysis, I recorded 87 soft calls from 18 males (1–13 per male, mean = 4.7). Samples were recorded with a Sennheiser K6/ME 62 microphone recording to an Edirol R9 portable recorder (frequency response: 20–22 000 Hz; quality of files: PCM, 48 kHz, 16 bits), 5–12 m from males. After recording, the males were caught using mist nets and ringed, and basic morphometric measurements were collected. I used tarsus length (mm) as a proxy of male size and its quality.

The call samples for Experiment 1 and Experiment 2 were initially prepared to match a 96 ± 5 dB sound pressure level (SPL) at 1 m for broadcast calls (natural level: mean = 96 dB, range 80–101 dB) and a 70 ± 5 dB SPL at 1 m for soft calls (natural level: estimated range, 65–76 dB). Broadcast calls have different structures than soft calls (Ręk, 2013), and their

function in the playback experiments was only to focus the attention of the focal male because soft calls alone might be too quiet. Broadcast calls are loud and easy to locate, and males produce them almost continually throughout the night. Hence, including them in playbacks gave all of males an opportunity to locate the speaker, regardless of the current conditions and habitat structure. SPL(A) was measured with a CHY 650 sound pressure level meter (Ningbo, China). All of the call samples were digitised, and acoustic manipulations carried out using the Avisoft SASLab Pro (Specht, 2007) sound analysis package (48 kHz/16 bit PCM files).

For Experiment 1 and Experiment 2 playbacks, I used a Creative ZEN player (quality of files: PCM, 48,000 Hz, 16 bits) connected to a Sekaku WA-320 loudspeaker (Taichung, ROC Taiwan) with a 20 W amplifier and 50–15 000 Hz frequency range. For recording, I used one microphone (Sennheiser K6/ME 67) connected to an Edirol R9 Portable Recorder (quality of files: PCM 48 kHz, 16 bits) during Experiment 1 and a digital Canon XA10 camcorder (quality of files: MPEG4-AVC/H.264, 1920×1080, 24 Mb/s; PCM 48 kHz, 16 bits), with an infrared recording mode connected to a microphone (Sennheiser K6/ME 67) during Experiment 2.

Experiment 1

Assuming that variability in the fundamental frequency is a predictor of male size, this experiment aimed at testing for differential responses of receivers to the natural variability in the fundamental frequency of gurgling notes.

In the playbacks, I used 204 samples of soft calls (single calls) recorded from 34 males (6 soft calls per male) and 34 samples of broadcast calls recorded from the same 34 males. The calls were recorded in 2007 and 2008, approximately 250 km south-west of the study area.

Each playback ($N = 34$) consisted of three 20-s recordings of broadcast calls, separated by two 20-s intervals. In addition to broadcast calls, the playbacks contained one soft call during the first interval (approximately 30 s into the stimulus), two soft calls during the second interval and three soft calls during the 20-s interval after the third playback of broadcast calls. Soft calls were evenly distributed within the time allotted, and they made up 5.6–7.1% of the vocalizations used in the playbacks. At the same time, gurgling notes retained their natural variability in fundamental frequency both within and between playbacks (see Results). The broadcast and soft calls employed in each playback came from the same male and the same recording. The trials lasted 140 s each, including the time for data collection after the last playback. Before each trial, the loudspeaker was placed 0.5 m above the ground within the subject male's territory. Experiments were carried out from the shortest distance possible, which meant that the male was approached as long as

its calling did not appear to be interrupted, but at no less than 5 m from the male (5–11 m). The trials were carried out by two persons: one responsible for sound recording and the second responsible for playback. Both persons monitored the males' motions. The person responsible for playback stood hidden approximately 2 m from the speaker, and he could monitor the behaviour of the focal birds in the close vicinity of the speaker.

Experiment 2

This experiment was aimed at testing for differential responses of receivers to the variability in the fundamental frequency of gurgling notes by decreasing the costs of signal assessment by receivers. In total, I used 176 samples of soft calls (single calls) and 44 several-minute-long samples of broadcast calls, all of which were recorded from 44 different males (4 soft calls and 1 sequence of broadcast calls per male) between 2007 and 2013 at a distance of up to 250 km from the study area.

Under natural conditions, males have a chance of hearing soft calls produced from different directions and distances and under different local acoustic conditions (e.g. in the presence of water), and at irregular time intervals or only a single calls. This makes comparison nearly impossible and assessment costly. During each trial ($N = 44$), the focal males received playbacks of four soft calls, separated by three 5-s intervals. Such sequences of soft calls are natural, and males regularly produce soft calls in series. Within each playback, three of four soft calls were modified, and the fourth soft call functioned as the control call. The modifications applied to the soft calls included (i) an increase of the fundamental frequency of gurgling notes by 20 Hz (Hz+ stimuli), (ii) an increase of the amplitude of gurgling notes by 20 dB (dB+ stimuli) and (iii) both an increase of the fundamental frequency by 20 Hz and an increase of the amplitude of gurgling notes by 20 dB (Hz+dB+ stimuli). The sequence of modifications was random within playbacks, and each playback contained calls with all three types of modifications. Additionally, the broadcast and soft call samples for each playback came from the same male.

The basic strategy underlying these modifications was to create a natural contrast in frequency and amplitude so that males could compare them but at the same time not to create an unnatural impression that consecutive stimuli come from different intruders. Hence, the modifications were relatively small, and both the fundamental frequency and amplitude remained within their natural ranges. To decrease the cost of assessment, males received different types of stimuli in short intervals. Consequently, not only could they directly compare calls, but they also remained in a very similar position relative to the playback speaker and were

subjected to comparable acoustic conditions during the whole stimulation period. To accomplish such an effect, the males must have been in a set position before the right stimulation, so that their behaviour could be observed immediately after receiving the stimuli. In this experiment, the loudspeaker was placed approximately 0.5 m above the ground before each trial, within the subject male's territory (15–30 m). Additionally, the small area around the speaker was trampled down, and some obstacles were removed for better visibility. To lure a male close to the speaker, I used loud territorial broadcast calls, which were played back for no longer than five minutes. Playback with soft calls began as soon as a male could be seen from the LCD screen or viewfinder of the camcorder, which was 2–4 m from the hidden researcher.

Assuming that variability in the fundamental frequency is a predictor of male size, Hz+ stimuli should provoke less aggression than control stimuli. I decided to increase the frequency instead of decreasing it because birds do not hear well at low frequencies (Dooling, 2002), and there was a risk that calls with especially low frequencies might go undetected. Considering the high level of background noise and the variability of the amplitude among soft calls due to sound degradation (Rek, 2013), it was crucial to separate the effect of the frequency from the effect of the amplitude, especially if the amplitude by itself can play important role in the settlement of territorial conflicts (Brumm & Ritschard, 2011). Such separation was achieved by the use of dB+ and dB+Hz+ stimuli. The first stimulus controlled for the effect of the amplitude per se, whereas the second tested whether the frequency can be adaptive considering the high variability in the amplitude of the signal. Because the mewing note of the soft call is the main contributor to its SPL (Rek, 2013) (Fig. 1), the 20 dB amplification of gurgling notes affected the amplitude of whole soft calls to a much lesser degree than the amplification of whole soft calls might affect the amplitude of gurgling notes.

Data analysis and statistics

For the bioacoustic analyses, I used the Avisoft SASLab Pro sound analysis package. For the analysis of video recordings (Experiment 2), I employed Observer XT 11.5 (Noldus IT) software.

For Experiment 1, I coded the responses of the males to playback into a three-step (1–3) ordinal multinomial variable. The response was categorized as 1 when a male reacted to playback weakly, that is when it moved sideways or backward, or when it stopped calling after playback and remained motionless. The response was categorized as 2 when a male changed its position towards the speaker. Finally, the response was categorized as 3 when a male physically attacked the playback speaker, and this category included behaviours such as

pecking, kicking and wing striking. Consequently, this classification reflected an increasing level of aggressiveness in males. During Experiment 2, the behaviour of the males was analysed only during the intervals of silence between consecutive soft calls and for 5 seconds after the last call was played back. The response of males was coded in the same way as in Experiment 1.

To analyse comparative morphometric bioacoustic data, I used linear mixed models. Within the models, the fundamental frequency [Hz] of gurgling and mewing notes were dependent variables, although the male was used as the random factor, and tarsus length was employed as the fixed covariate. To analyse the influence of the fundamental frequency of gurgling notes from natural soft calls on males' aggressiveness (Experiment 1), I used a generalized linear model (GLM) with a multinomial distribution and probit link function. To analyse the effect of an increased frequency and amplitude of the fundamental frequency of gurgling notes on males' aggressiveness (Experiment 2), I employed generalized estimating equations (GEE), which can handle repeated measures of ordinal multinomial data. Within the model, the within-subject correlation among the responses of males to different playback stimuli was controlled, with the male being used as the subject variable and the sequence of playback stimuli (Hz+, dB+, Hz+dB+, control; in any order) as the within-subject variable. All statistics were calculated in SPSS v21.0. All *P* values are two-tailed.

Results

Potential of frequency for signalling

The correlations between tarsus length (mean \pm SD = 45.6 ± 1.5 mm) and the fundamental frequency differed significantly between soft call notes (Fig. 2). Among mewing notes, the frequency was basically independent of male size, whereas bigger males produced gurgling notes with significantly lower frequencies (between-subject mean: mean \pm SD = 204.6 ± 49.0 Hz; within-subject standard deviation (calculated only from 11 males with 3+ calls): mean \pm SE = 29.1 ± 8.8 Hz; Table 1).

Responses to natural soft calls

Males subjected to a series of natural soft calls were exposed to a similar variability in the fundamental frequency of gurgling notes (between-subject mean: mean \pm SD = 190.5 ± 41.7 Hz) to the variability recorded among captured males (Levene's test for equality of variances: $F_{50} = 1.16$, $P = 0.287$). This means that the potential of the frequency for predicting male size must have been similar in both cases.

In total, 26.5% ($N = 9$) of the males attacked the speaker, whereas 38.2% approached the speaker

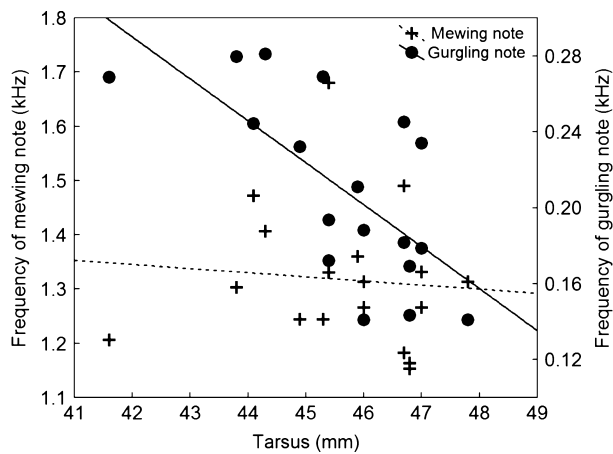


Fig. 2 Relationships between the fundamental frequency of soft call notes and the length of males' tarsuses.

Table 1 Effects of tarsus length on the fundamental frequency of soft call notes.

	Estimate	SE	d.f.	<i>t</i>	<i>P</i>
Gurgling					
Intercept	1153.7	275.4	19.18	4.19	<0.001
Tarsus	-18.9	6.6	16.55	-2.85	0.011
Mewling					
Intercept	1444.3	994.4	18.63	1.45	0.163
Tarsus	-3.1	21.8	18.63	-0.14	0.890

Mixed model regression parameters with fundamental frequency [Hz] as dependent variable.

($N = 13$), and 35.3% of the males responded weakly to playback ($N = 12$). However, it appears very unlikely that these responses had anything in common with the fundamental frequency of gurgling notes (score 3: mean \pm SD = 202.2 \pm 50.7 Hz, score 2: mean \pm SD = 174.6 \pm 31.9 Hz, score 1: mean \pm SD = 198.9 \pm 41.8 Hz; correlation between the frequency and response score: $r_s = -0.023$, 95% confidence interval of r_s : $-0.395 - +0.361$, $P = 0.897$). Additionally, a model including frequency as a covariate showed much higher information criteria than the intercept-only model (AIC = 72.17 vs. AIC = 11.44), which strongly suggests that frequency was practically passed over in the males' decisions and did not have any signalling value for receivers.

Responses when the cost of assessment was decreased

The focal birds responded most aggressively towards dB+ stimuli and least intensively towards Hz+ stimuli; 14 males responded weakly to all types of soft call stimuli (Fig. 3). However, the frequency was the only factor

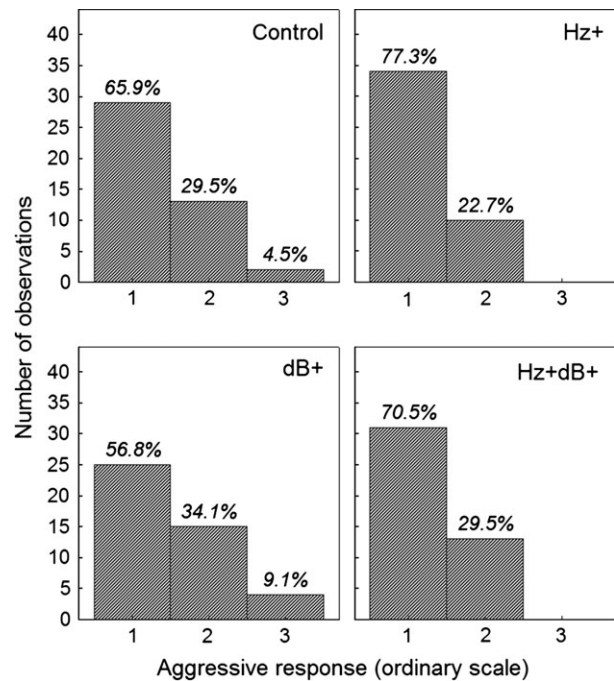


Fig. 3 Distributions of the responses of males to four stimulus types. The higher the value of the score, the greater the aggressiveness of the responses. The response variable: = 1 when a male reacted to playback weakly, = 2 when a male changed its position towards the speaker and = 3 when a male physically attacked the playback speaker (see Methods for details).

in the model that significantly affected the responses of focal males (Table 2). In addition, the very nonsignificant interaction effect showed that changes in amplitude had no signalling value independent of the frequency.

Discussion

This study shows that it is more beneficial for corn-rakes to respond to signals that are cheaper regarding assessment but are stabilized with a mechanism that is prone to a high level of cheating, rather than to signals that are costly for assessment but are stabilized with a

Table 2 Factors associated with male aggression after the cost of assessment was decreased.

	Wald χ^2	d.f.	<i>P</i>
Amplitude	2.41	1	0.121
Frequency	7.92	1	0.005
Amplitude \times Frequency	0.06	1	0.804

GEE model including amplitude (increased, unchanged) and frequency (increased, unchanged) as factors and aggressive score (1–3) as dependent variable.

highly reliable mechanism. The fundamental frequency of gurgling notes was a strong predictor of male size. However, this association was ignored by receiver males during simulated territorial intrusions. In contrast, the males appeared to respond indiscriminately to soft calls, which has been shown for this species previously (Ręk & Osiejuk, 2011). The most parsimonious conclusion, then, is that the fundamental frequency of gurgling notes does not act as a signal under natural conditions. Nevertheless, the data from Experiment 2 showed that the fundamental frequency is attended by receivers and therefore becomes a signal only if the cost of its assessment by receivers is slightly decreased. Even when the playback stimuli differed by only 20 Hz, which is rather a small difference considering the natural variability among males, receivers responded to the frequency differentially provided they could directly compare signal variants. In other words, the males responded as soon as the assessment of the signal variants could be performed rapidly and straightforwardly, means that the assessment was cheap. Thus, these results follow studies suggesting that costly signals are not evolutionarily stable against the invasion of cost-free signals (Számádó, 2003) by supporting the long-standing hypothesis (minimal cost hypothesis) that signalling systems are always prone to dishonesty due to the effects of the costs of assessment paid by receivers and will be replaced by cheaper and more susceptible to cheating signals (Dawkins & Guilford, 1991).

Previous research has demonstrated that the soft calls of the corncrake are predictors of the signaller's aggression, with reliability being maintained by receiver retaliation (Ręk & Osiejuk, 2011), but this effect does not exclude the potential signalling value of the fundamental frequency for conflict settlement. Just the opposite, any reliable information regarding the sender is useful to the receiver, especially during antagonistic interactions and if that information concerns a critical parameter such as the size of the intruder. In fact, a vital role of the fundamental frequency in conflict resolution or mating has been shown in many groups of vertebrates (Behr *et al.*, 2009; Vannoni & McElligott, 2008; Wagner, 1989; Morton, 1977), and analogical acoustic, although nonvocal, functional predictors of male size have also been noted among invertebrates (Gray, 1997). Therefore, the lack of effect of the fundamental frequency observed in the first experiment, despite its proved potential, may appear to be surprising. The fact that in the second experiment, the amplitude of gurgling notes did not affect the males' aggressiveness suggests that signallers have little room for the manipulation of the amplitude of gurgling notes so that the fundamental frequency preserves its potential for signalling. Local acoustic conditions and especially noise levels can have an insidious effect on the efficiency of low-frequency signals (Halfwerk *et al.*, 2011; Ręk, 2013). Hence, the frequency structure of gurgling notes may represent an

evolutionary dead end because there may exist no combination of acoustic parameters with costs of production paid by senders and costs of assessment paid by receivers for which communication would be beneficial for both senders and receivers.

Following theoretical conclusions (Dawkins & Guilford, 1991; Lachmann *et al.*, 2001; Számádó, 2010), the results showed that signals do not have to be costly to produce to be functional during conflicts over high-value resources, which suggests that signal honesty is not an absolute precondition for communication. According to Zahavi's handicap principle (Zahavi, 1975), which is one of the proposed mechanisms for signal selection, signals should be honest and costly (wasteful), and they should be costlier for poorer signallers (Grafen, 1990). The soft calls of the corncrake meet the first of Zahavi's criteria, at least on average (Ręk & Osiejuk, 2011). However, it is not the cost of production that makes these calls reliable (Experiment 1) but the punishment by receivers. Dawkins and Guilford (Dawkins & Guilford, 1991) predicted that the costs receivers pay in assessing the signal may reduce the honesty of the signal because it may be more advantageous for receivers to accept some level of dishonesty and to pay less for the occasional assessment of cheap signals, rather than to pay for the honest assessment of costly signals (but see Polnaszek & Stephens, 2014). This study did not test the incidence of dishonest signalling; however, it indicated that the maintenance of signal honesty does not have to be a wasteful process, as predicted by Zahavi's theory, and can instead be a cheap process involving a simple frequency-dependent mechanism – the retaliation rule (Molles & Vehrencamp, 2001). Such a mechanism is less consistent than Zahavi's handicap because of a higher incentive to cheat; however, ambiguity is not a necessary consequence of cheap signalling. In fact, it can be more beneficial to signal honestly to avoid the potential costs of signalling out of equilibrium because the signals used at equilibrium do not have to be costly (Lachmann *et al.*, 2001).

The above conclusions point to the active role of signal receivers for the evolution of animal communication. In recent years, there has been an extensive discussion on the role of receivers/perceivers in communication (Stegmann, 2013). Advocates of the first option understand signalling in terms of influence and communication as the manipulation of perceivers by senders (Owren *et al.*, 2010; Rendall *et al.*, 2009). Conversely, their opponents link communication to a large degree with information processing and consider receivers to play the more active role of assessors (Seyfarth *et al.*, 2010; Bradbury & Vehrencamp, 2011). The difference is not trivial, as the first group regards signals mainly as consequences of sensory biases, whereas the second group believes that receivers act nonrandomly with respect to the state of the signal, which means that receivers can shape signals through senders'

behaviour for their own benefits, in addition to senders' benefits. My results showed that receivers can ignore the signal if signal assessment is not beneficial for them. Therefore, it would not be appropriate to limit the influence of the frequency of gurgling notes on the receivers in Experiment 2 only to sensory bias that pre-dates the evolution of gurgling notes. However, the tested signal is based on a simple association between sound frequency and male size, its communication did not appear to have the character of a mechanistic influence, being beneficial only for signallers. Instead, more likely it emerged as a consequence of adaptations in both signallers and receivers (Scott-Phillips *et al.*, 2012).

My findings contribute to the expanding field of research on soft vocalizations. (reviewed in: Osiejuk, 2011; Searcy *et al.*, 2014). Soft songs and calls have been shown to be reliable predictors of attack in multiple species, including songbirds (Searcy *et al.*, 2014) and corncrakes (Ręk & Osiejuk, 2011). Because it is unlikely that low amplitude is a factor that should make a vocalization more costly to produce by itself, it has been accepted that such signals have low intrinsic costs and are stabilized by a receiver-dependent cost. Nevertheless, the topic is far from being closed, and this research complicates it even more because it suggests that the acoustic structure of soft vocalizations is not necessarily neutral for their function and that it is not only the amplitude that makes these vocalizations so effective. So far, multiple researchers carried out playback experiments to demonstrate the adaptive significance of soft vocalizations, but few tested the environmental and physiological constraints on their production (Ręk, 2013; Ręk *et al.*, 2011; Dabelsteen *et al.*, 1998). Hence, we should focus more on vocalizations themselves before generalisations are possible.

In summary, my findings provided evidence that there is a trade-off between signal honesty and assessment cost in which receivers settled for less costly but not perfectly honest signals. I found that on the one hand, males ignored the fundamental frequency of the calls, despite the fact that it was informative about the size of the signaller. On the other hand, manipulated calls with increased fundamental frequency made receivers to behave more cautiously, which implies that signaller and receiver might accept some level of signal dishonesty by choosing signals cheaper in assessment but stabilized with less a reliable mechanism. In the end, these results suggest that from the receiver's perspective, a signal does not have to be absolutely honest, but it must above all be beneficial.

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