Behavioral Ecology
doi:10.1093/beheco/arr027
Advance Access publication 4 April 2011

Original Article

Nonpasserine bird produces soft calls and pays retaliation cost

Paweł Ręk and Tomasz S. Osiejuk
Department of Behavioural Ecology, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland

Low-amplitude vocalizations produced during aggressive encounters, courtship, or both (quiet/soft songs) have been described for many species of song-learning passerines; however, such signals have not been studied among nonlearning birds. During aggressive interactions, apart from using the broadcast call, male corncrakes (*Crex crex*) produce a low-amplitude, gurgling–mewing call, which appears to be equivalent to soft songs of songbirds. Previous studies have shown that low-amplitude vocalizations are reliable signals of aggressive motivation. It is unclear, however, how the reliability of such signals is maintained. We experimentally tested whether males that use soft calls are more likely to attack later on and whether males respond differently to natural calls consisting of both broadcast and soft elements and to their modified versions where the soft elements were removed. Senders were more likely to attack the speaker if they earlier produced soft calls. Receivers were more likely to attack the speaker or retreat the speaker if the playback included soft calls. These results show that soft call is a signal of aggressive motivation in the corncrake, and we argue that the reliability of this signal is maintained by a receiver-retaliation rule. *Key words:* aggressive signal, *Crex crex*, retaliation rule, soft call, soft song. *[Behav Ecol 22:657–662 (2011)]*

INTRODUCTION

Because one of the main functions of birdsong is female attraction, a majority of songs are characterized by relatively high amplitude (Naguib and Wiley 2001). What is more, such signals are not directed at a specific receiver but rather at anyone who can hear them. Conversely, apart from regular songs, some species produce quiet songs that appear to be quiet not because they cannot be sung louder but because it is beneficial for a bird to sing them quietly. Such songs have been detected during courtship, aggressive encounters, or both when the distance between the sender and receiver was relatively small (Dabelsteen and Pedersen 1988, 1990; Lampe 1991; Dabelsteen et al. 1998; Morton 2000; Anderson et al. 2008). Hence, they appear to have a short-distance character. Signals of this kind are variably termed (e.g., soft songs), and most of them are quiet versions of broadcast songs (with or without structural differences) or low-amplitude songs that do not have loud counterparts (Dabelsteen et al. 1998; Anderson et al. 2008; Ballentine et al. 2008).

From a theoretical point of view, signals should be on average reliable (Fitch and Hauser 2003; Maynard Smith and Harper 2003). Research to date has shown that during agonistic interactions, soft songs are strong and reliable signals of aggressive motivation in male song sparrows (*Melospiza melodia*), swamp sparrow (*M. georgiana*) (Searcy et al. 2006; Ballentine et al. 2008), and the black-throated blue warbler (*Dendroica caerulescens*) (Hof and Hazlett 2010). Paradoxically, the high reliability of signals is the main reason why weak individuals should try to use them unreliably. Therefore, if signals are reliable on average, it means that either they cannot be faked (Maynard Smith 1979; Maynard Smith and Harper 2003) or that senders must pay a cost that outweighs the possible benefits from cheating (Zahavi 1977; Enquist 1985; Grafen 1990). A few hypotheses have been proposed to explain what evolutionary mechanism maintains the reliability of soft songs during aggressive encounters (Searcy et al. 2006; Anderson et al. 2007). The conclusions from the research, however, do not argue definitely for any hypothesis (Vehrencamp 2000; Anderson et al. 2007; Laidre and Vehrencamp 2008; Searcy et al. 2008; Searcy and Beecher 2009).

Firstly, the cost that stabilizes low-amplitude vocalizations may be paid via a receiver-retaliation rule (Enquist 1985). According to this rule, cheaters signaling high aggressiveness should pay the highest retaliation cost (while being attacked by a truly strong male). Strong males should test the honesty of senders because a strong male has more to lose by being cheated by a weak male than in risking fights with any male (Hurd 1997). Moreover, the fights should be the most severe for closely matched opponents (Hurd 1997). The application of the retaliation rule has been demonstrated for song-type matching in the banded wren (*Thryothorus pleurostictus*) and song sparrows (*M. melodia*) (Burt et al. 2001; Molles and Vehrencamp 2001; Vehrencamp 2001), and it has also been suggested for song-type switching rate in song sparrows (Vehrencamp 2001). Conversely, analogous research on soft songs in song sparrows gave insignificant results (Anderson et al. 2007; but see Searcy and Beecher 2009). Secondly, it was suggested that a male producing low-amplitude vocalizations necessarily places itself in a position of vulnerability to attack and injury by the receiver (Vehrencamp 2000; Laidre and Vehrencamp 2008). According to the vulnerability hypothesis, the signal is reliable because only strong and confident males can accept a high risk of injury (Zahavi 1977). Hence, short range and low-amplitude songs appear to match the assumptions of the vulnerability hypothesis (Laidre and Vehrencamp 2008). Nevertheless, this hypothesis was thoroughly criticized (Searcy et al. 2008), mainly because soft songs by no means

Address correspondence to P. Ręk. E-mail: rek@amu.edu.pl.
Received 5 December 2010; revised 18 February 2011; accepted 19 February 2011.

increase the likelihood of injury (above the risk of attack) compared with broadcast songs. Finally, it was proposed that the stability of soft songs is achieved because males communicating quietly with rivals must at the same time cease attracting or courting females (Anderson et al. 2007) or risk other males trespassing into their territories (Searcy and Nowicki 2006). This cost is therefore strictly dependent on the total time spent on quiet singing, which seems likely to be small (Anderson et al. 2007).

The corncrake (*Crex crex*) is a territorial polygynous rail, inhabiting dense marshy grasslands. Males are active and call mostly during the night. Because males cannot see one another until they are very close, their communication system is likely to be based on acoustic signals. Males are known from their disyllabic loud cracking calls (ca. 96 dB) (hereafter, broadcast calls; Figure 1a,c) that are easily heard from a distance of up to 1–1.5 km (Schäffer and Koffijberg 2004). It was shown that the intermittent rhythm of these calls (Figure 1c) communicates the aggressive motivation of males (Ręk and Osiejuk 2010). Additionally, corncrakes produce gurgling–mewing calls (hereafter, soft calls), which are structurally disparate from broadcast calls (Figure 1a,b) and which are used during sexual displays and during aggressive interactions (Cramp and Simmons 1980; Schäffer et al. 1997; Schäffer and Koffijberg 2004). Soft calls are low-amplitude signals (ca. 70 dB), they have short range (about 15 m) and they are produced from a short distance (mean distance to the speaker ± standard deviation [SD] = 4.5 ± 4.4 m). Therefore, it seems plausible that soft calls in the corncrake and soft songs used by songbirds are equivalent signals. The potential finding that low-amplitude calls are reliable about impending aggression in a nonpasserine species, in addition to the findings and widespread occurrence of soft songs in aggressive situations in passerines, might suggest that there is something uniquely advantageous about soft vocalizations.

The aim of this study was to test experimentally whether soft calls in the corncrake meet the conditions of aggressive signals and to establish whether soft-calling corncrakes pay retaliation cost. We tested these ideas in 2 separate playback experiments with similar setups that simulated intrusions of a nonneighbor male into the focal male's territory. To establish that a given signal is aggressive, it is necessary to examine both what the signal means to the signaler (sender's perspective) and what the signal means to the receiver (receiver's perspective) (Vehrencamp et al. 2007; Searcy and Beecher 2009). From the sender's perspective, the signal is aggressive when it predicts subsequent aggressive escalation. Nevertheless, the coincidence of the signal and aggressive behavior does not prove that receivers understand the meaning of the signal. From the receiver's perspective, it can be proved that the signal is salient to the receiver, but it cannot be resolved whether the signal is aggressive or nonaggressive (Searcy and Beecher 2009). In the first experiment (E1), we confronted males with playback stimuli that elicit aggression and investigated the behavior of senders. We asked whether corncrakes that use soft calls are more likely to attack soon after. In the second experiment (E2), we used soft call and control stimuli to compare reactions of the receiver in a paired design. E2 had 2 functions: to strengthen the evidence for the aggressive function of soft calls (demonstrating that soft calls are salient to males) and to specifically test the retaliation rule hypothesis. According to this hypothesis, receivers should, on average, respond more aggressively to soft calls compared with broadcast calls; hence, the cost being enforced by the receiver's aggressive response. Nevertheless, it is difficult to interpret the outcome of playback experiments, which test for a cost in this way, because a highly aggressive signal might provoke attacks from some individuals and retreats from others (Popp 1987; Mennill and Ratcliffe 2004; De Kort et al. 2009; Ręk and Osiejuk 2010). The reason for this difficulty is the fact that the most effective signal should be the most costly (Enquist 1985), and thus, the signal that is the most likely to incite some receivers to attack should be the most successful in causing other receivers to retreat (Searcy and Nowicki 2005). Therefore, if soft calls are threats stabilized by retaliation cost, they should increase the frequency of attacks by receivers, but they also should increase the frequency of retreats by receivers.

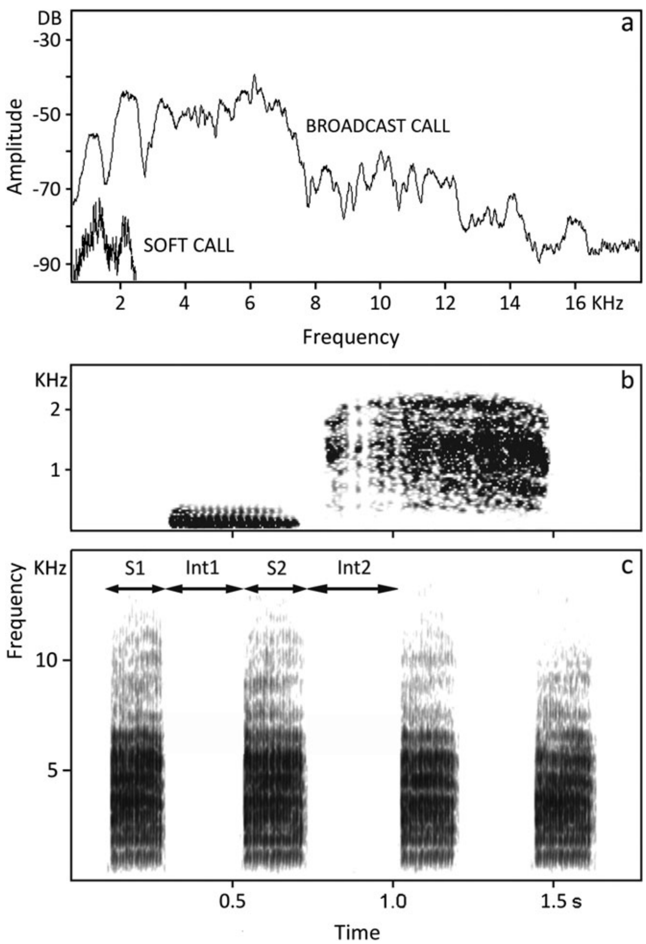

Figure 1
Frequency spectra and sonograms of corncrake calls used in playbacks: (a)—frequency spectra of soft and broadcast calls; (b)—soft call sonogram; and (c)—broadcast calls sonogram. It has become customary to think that broadcast call consists of 2 syllables/vocalizations and 2 intervals (S1, Int1, S2, Int2). The rhythm of the broadcast calls was defined as the ratio of the length of the second interval (Int2) to the sum of the lengths of the first syllable (S1), first interval (Int1), and second syllable (S2)

MATERIALS AND METHODS

Study area and subjects

Playback experiments carried out in Northeast Poland in Biebrza National Park, its surroundings, and southwards from the park (the outermost coordinates: 53.61934 N, 53. 12642 N, 23.01035 E, 22.36065 E) from 17th May through 2nd June in 2009. The study area consisted of meadows and marshes with wet and boggy soils to the north and meliorated mineral soils to the south. The average temperature (measured between 2200 and 2300 at ground level) was 13.9 ± 2.8 °C (mean ± SD). The subjects were 63 territorial male corncrakes. The subjects were individually recognizable because intervals between maximal amplitude peaks in syllables of male broadcast calls (pulse-to-pulse duration) are stable for longer periods and can be used as fingerprints (Peake et al. 1998; Peake and McGregor 1999).

Experiments, treatments, and playback protocol

Calls for playbacks were recorded in 2007 and 2008 (about 250 km southwest of the study area). Calls were digitized using the Avisoft SASLab Pro 4.52 (Specht 2007) sound analysis package (48 kHz/16 bit PCM files). Each playback sample was 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 71 ± 5 dB (SPL at 1 m) for soft calls (natural level: range 65–76 dB; the amplitude of background noise in the corncrake's habitat in June exceeds 60 dB). These natural amplitudes were measured earlier for several males calling at known and small distances (<2 m) (with a CHY 650 [Ningbo, China] sound pressure level meter).

The key response variable was "attack," defined as a body strike on the speaker (or any clump of vegetation adjoining the speaker). Because interactions between corncrakes take place within a very dense and dark environment, males cannot rely on visual cues, and they attack abruptly any source of playback. Attacking is a violent and unambiguous behavior. It consists of a fast movement toward the source of the playback, strikes of wings, and pecking. We also recorded motions of males (approaches and retreats) and rhythm of broadcast calls (before the playback). We accepted that a male approached if it came to less than 3 m from the speaker, and it was closer to the speaker at the end of the experiment than at the beginning. We accepted that a male retreated if at the end of the experiment it was further from the speaker than at the beginning, and it did not approach the speaker during the experiment. Because some males retreated quietly or flew away and did not call after that, we were unable to detect precisely the moment of retreat and/or to estimate the distance of retreat; we could only check after the experiment the presence or absence of a male in its last known location (up to 5 m around). Experiments were carried out between 2200 and 0215 h local time. Playback calls were broadcast through the amplified loudspeaker (20 W, frequency range 50–15 000 Hz; SEKAKU WA-320, Taichung, Republic of China Taiwan) connected to a Creative ZEN player. For recordings, we used 1 omnidirectional microphone recording to an Edirol R9 Portable Recorder. Before each experiment, the loudspeaker was placed <0.5 m above the ground within the subject male's territory. Experiments were carried out from the smallest distance possible, which means that we approached the male as long as its calling did not seem to be interrupted by our presence or until we could assess relatively well its position. In the second case, we did not approach to less than 5 m from the male (5–11 m). Experiments were performed by 2 persons: one responsible for sound recording and the second responsible for playback. Both persons monitored males' motions. The person responsible for playback stood about 2 m from the speaker, and he could monitor the behavior of focal birds in the close vicinity of the speaker.

To examine the behavior of senders (E1), we confronted subject males ($n = 29$) with territorial playbacks ($n = 29$ playbacks, each coming from a different male), and we recorded signals given, motions, and attacks. Each male was subjected to one playback treatment with broadcast calls. Playbacks did not contain soft calls because they were not intended to threaten a subject but only to imitate the presence of an intruder within the subject's territory. Each experiment lasted 140 s and consisted of three 20-s playbacks, separated by two 20-s intervals, and followed by additional 40 s without playback allocated to males' reactions. We started the playback as soon as we recorded a male calling (at least 20 s of broadcast calls). The calls used in each experiment came from a single male. To avoid the potential confounding effect of the rhythm of broadcast calls (see Figure 1 for definition), we selected the calls with similar rhythm (mean = 0.83, range: 0.81–0.87; ca. natural range: 0.4–1.3).

In E2, in which we examined the behavior of receivers, each male ($n = 34$) was subjected to 2 playback treatments (experimental treatment with soft calls and broadcast calls, i.e., SOFT and control treatment with broadcast calls, i.e., CONTROL) that were conducted in a random order on 2 consecutive nights. Broadcast calls make up a natural background (default behavior) for the interactions in the corncrake. We included broadcast calls in playbacks because males produce them almost continually throughout the night (even during interactions), making pauses only for soft calling (if producing any), listening, and while moving. Because broadcast calls are loud and easy to localize, we wanted to give all males equal opportunity to localize the speaker regardless of current conditions and habitat structure. At the same time, because broadcast calls can be used to signal aggressive motivation (Ręk and Osiejuk 2010), to provide males with the same amount of information in both treatments, a sample of broadcast calls used in the CONTROL treatment was selected on the basis of the similarity of its rhythm to the rhythm of broadcast calls from the SOFT treatment, and both treatments for a subject always contained identical numbers of broadcast calls (depending on the rhythm and length of syllables, it was 84–108 syllables, mean = 97.2). It should be noted, however, that the function of broadcast calls in E2 was not to control or duplicate the effect of soft calls (we did not plan to test the difference between these 2 calls) but only to focus the attention of the focal male (soft calls alone might be too quiet, and they have no loud counterparts). We accepted that to control the effect of an intruder that stops producing broadcast calls in order to produce soft calls (natural situation imitated by SOFT treatment), one needs to imitate the effect of an intruder that stops producing broadcast calls and falls silent (i.e., that behaves identically in any other way—situation imitated by CONTROL treatment). Experiments lasted 140 s each. Each one consisted of three 20-s playbacks of broadcast calls, separated by two 20-s intervals, and followed by another 40-s interval without broadcast calls. In the CONTROL treatment intervals and the final 40 s of the experiment did not contain any calls. In addition to broadcast calls, the SOFT treatment contained 1 soft call during the first interval (after about 30 s into the stimulus), 2 soft calls during the second interval, and 3 soft calls during the first 20 s 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 vocalizations used in the SOFT playbacks.

In sum, we used 34 SOFT and 34 CONTROL samples, each coming from different males. Broadcast and soft calls for each SOFT came from the same male and the same recording, whereas broadcast calls from a pair of SOFT and CONTROL treatments used with 1 male came from different males.

Statistical analysis

For the analysis of the data from E1, we used X^2 test with Yates' correction for continuity to test the effect of soft calls on signalers' subsequent behavior and Mann–Whitney test to

Table 1

The number of males attacking and approaching the speaker among soft-calling and non–soft-calling males

	Attack (2.5)	Approach, no attack (1.4)	No attack, no approach (0)
Soft call	5	5	0
No soft call	1	0	18

$N = 29$, each individual belongs to one category. The numbers in brackets are mean numbers of soft calls produced by attackers, approaching nonattackers, and nonapproaching males.

Table 2

The numbers of males that attacked, retreated or did not respond during BROADCAST and SOFT treatments

		CONTROL		
		Attack	No attack, no retreat	Retreat
SOFT	Attack	2	7	0
	No attack, no retreat	0	15	0
	Retreat	0	9	1

$N = 34$ males, the same individuals are included in SOFT and CONTROL treatments. The matched pair is the unit of the table, and pairs are classified according to whether or not the member of that pair behaved in a given way during both treatments, for example, 7 males that attacked during SOFT treatment did not respond to playback during CONTROL treatment.

compare rhythm of broadcast calls between attackers and nonattackers. For the X^2 test, we collated the data in 2 contingency tables in which we compared 1) the number of attackers and nonattackers among soft-calling and non–soft-calling males and 2) the number of males approaching and nonapproaching (including retreating males) the speaker among soft-calling and non–soft-calling males. Additionally, we performed a forward stepwise probit regression (generalized linear model) to compare the influence of soft calls (dichotomous variable) and rhythm of broadcast calls before playback (continuous variable) on subjects' aggressiveness.

For the analysis of the paired data from E2, we used generalized estimating equations (GEE). The models and parameters were selected using the quasi-likelihood under independence model criterion (for choosing the best correlation structures) and its corrected version (for choosing the best subsets of predictors). We performed 2 separate analyses with 2 binomial dependent variables: attack and retreat. During the model-fitting process, we used the following categorical variables and covariates: treatment (SOFT vs. CONTROL), distance (of subjects to the speaker when playbacks were started), and the number of vocalizations per playback (including soft and broadcast calls). All P values are 2-tailed. All analyses were performed in SPSS 16.0 software.

RESULTS

In E1, we analyzed the association between the signals of focal birds and the signalers' subsequent behavior. Table 1 shows frequencies of males' responses during experiments. Birds producing soft calls were more likely to attack the speaker than birds nonproducing soft calls (Table 1; $X^2 = 5.50$, degrees of freedom [df] = 1, $P = 0.019$). Similarly, males calling with a more intermittent rhythm before the playback were more likely to attack the speaker than males calling with a more monotonous rhythm (rhythm of attackers: mean ± SD = 0.86 ± 0.06, rhythm of nonattackers: mean ± SD = 0.74 ± 0.13; Mann–Whitney test: $U = 26.0$, $P = 0.021$). However, soft call was the only variable that was retained in the final generalized linear model (Wald $X^2 = 5.83$, df = 1, $P = 0.009$). When we used approach to the speaker instead of attack as a weaker proxy of aggressive response, the effect of soft calls turned out to be stronger (Table 1; $X^2 = 21.11$, df = 1, $P < 0.0001$), which suggests that if we allowed for longer interactions even more soft-calling birds might attack the speaker (latency to approach among attackers: mean ± SD = 88 ± 13 s; latency to approach among approaching nonattackers: mean ± SD = 112 ± 13 s; $U = 4.0$, $P = 0.044$). It should be underlined that all approaches and attacks took place after the playback started (mean latency to approach = 95 s [38–121]; mean latency to attack = 99 s [40–137]), and in all cases (except for one male that approached and attacked without soft calling), males first uttered soft call(s) and later either approached or approached and attacked.

In E2, we analyzed the responses of receivers to different playback treatments. Table 2 shows the numbers of subjects that attacked or retreated during SOFT and CONTROL treatments. None of the subjects did both, which means that attackers and retreaters were different groups of birds. Birds were more likely to attack the speaker during SOFT treatment ($n = 9$, latency range: 80–134) than during CONTROL treatment ($n = 2$, latency range: 88–91) (Table 2; GEE: Wald $X^2 = 8.30$, df = 1, $P = 0.004$). Moreover, SOFT playbacks were more effective in causing receivers to retreat ($n = 10$ retreats during SOFT vs. $n = 1$ during CONTROL; Table 2; GEE: Wald $X^2 = 9.78$, df = 1, $P = 0.002$). In contrast, neither the distance of the birds when playbacks were started (mean ± SD = 7.6 ± 1.4) nor the number of vocalizations per playback affected males' responses, and both covariates were not retained in the final GEE models (all $P > 0.2$).

DISCUSSION

Low-amplitude calls produced by male corncrakes have the characteristics to be considered aggressive signals. Firstly, senders that produced soft calls were more likely to attack the speaker than senders that did not produce them, which supports the hypothesis that soft calls transmit aggressive information. In addition, soft calls were stronger predictors of attack than rhythm of broadcast calls. Secondly, different reactions of males to SOFT and CONTROL playbacks indicate that soft calls were recognized by males. The fact that the substantial number of males either attacked or retreated from the speaker during SOFT treatment suggests that males of different quality showed different behavioral responses to playbacks (see Popp 1987). Irrespective of the quality of the male, however, the conclusion is the same, namely, the signal is a threat, and our results provide strong justification that soft calls in the corncrake are reliable aggressive signals. Conversely, a number of birds did not attack, approach, or retreat the playbacks in both experiments, which might imply that these variables do not capture the whole spectrum of aggressive responses. In fact, the reactions of corncrakes to playback and simulated intrusions are graded (Ręk and Osiejuk 2010). Thus, it is likely that the extension of playback and, for example, the imitation of the intruder's move (e.g., using a few speakers) might increase the frequency of aggressive/submissive responses. It is also possible that males reacted differently to SOFT and CONTROL playbacks because SOFT playbacks contained more calls (5.9–7.6% more calls in SOFT playbacks relative to CONTROL playbacks) than CONTROL playbacks (see MATERIALS AND

METHODS); however, we think that this confound by itself is unlikely to have caused the effect seen in E2 (350% more attacks and 900% more retreats during SOFT treatment relative to CONTROL treatment) (Table 2).

Furthermore, our results support the hypothesis that soft-calling corncrakes pay retaliation cost. According to a receiver-retaliation rule (Enquist 1985), a weak individual pretending to be strong should pay the retaliation cost if it tries to deceive a strong individual. The costs of cheating should fall more heavily on individuals of low quality or fighting ability than on individuals of high quality or fighting ability (Enquist 1985; Searcy and Nowicki 2005). Therefore, the signal stabilized by retaliation cost should be effective both in helping the signaler to drive the receiver back and in provoking the receiver to attack (Popp 1987). It should be underlined here that retreating from the signal is not an argument against the social cost for soft calls. As long as a newcomer cannot predict the quality of the territory owner and its response (attack/retreat), it will pay, on average, the cost of retaliation. Conversely, the presence of attacks and retreats is an argument for social cost because a strong threat should be both beneficial for the honest sender and costly for the dishonest sender. The function of a threat is to intimidate an opponent, not to be punished. As long as there is no expected benefit from signaling honestly, there would be no cost of cheating, or in the opposite way, as long as senders pay the cost, on average, they must benefit, on average. Soft calls were both effective in provoking the rival to attack as well as in causing the rival to retreat, which exactly matches the assumptions.

However, this study tests specifically for the hypothesis that the reliability of soft calls is maintained by a retaliation rule, we acknowledge the possibility that multiple mechanisms could be contributing to the reliability of low-amplitude vocalizations. Similar to soft songs of passerines, soft calls of the corncrake are produced only in exceptional situations. Their production cost seems to be smaller than the cost of loud broadcast calls because of both lower amplitude and very low rate. Moreover, considering for example small cost of crowing in roosters (Chappell et al. 1995; Horn et al. 1995), production costs in terms of energy consumption of soft calls seem unlikely. Nevertheless, it might be technically (physiologically) demanding to produce soft vocalizations or there might be some developmental costs.

Except for retaliation 2 other kinds of costs were postulated with specific reference to soft vocalizations. Although singing quietly benefits the sender because it is helpful in driving trespassers off, it can be costly because it prevents the sender from loud singing for females and males. This so-called "competing functions cost" (Anderson et al. 2007; Ballentine et al. 2008; Searcy et al. 2008) could have quite substantial effect on fitness, if, for example, a third party male copulated with another male's mate; however, measuring this cost would be very difficult. It was shown in song sparrows that intrusions by third party males were more frequent if a territory owner produced soft songs and an intruder produced broadcast songs than if both males produced broadcast songs (Searcy and Nowicki 2006). In corncrakes, signaling during aggressive interactions is never restricted to soft calls but instead it comprises a mixture of broadcast calls, pauses (some males even fall silent), and soft calls (with a marginal share of the last). Therefore, we think that, even if competing functions cost plays any role in stabilizing the honesty of soft calls in the corncrake, it is a minor role.

Because soft vocalizations can only be transmitted when the sender is relatively close to the receiver, it was suggested that they are stabilized by a vulnerability cost (see for discussion: Vehrencamp 2000; Laidre and Vehrencamp 2008; Searcy et al. 2008;). According to the vulnerability hypothesis (Vehrencamp 2000), singing quietly should necessarily place the sender in an exposed position (risk of injury if an attack should occur) compared with singing loudly. Such an effect might be achieved if, for example, soft vocalizations informed clearly an opponent how close the sender is willing to come (Laidre and Vehrencamp 2008). Corncrakes produce broadcast calls both far from and close to each other. Hence, vulnerability hypothesis cannot explain why broadcast calling males start to produce soft vocalizations (see also Searcy et al. 2008).

One of the implications of this study is the extension of the use of soft vocalizations to a different taxon of birds. The fact that multiple taxa have converged on a similar signal form that conveys aggressive motivation may suggest that there might be something "special" about soft vocalizations themselves that enforces their reliability beyond a simple retaliation rule. McGregor and Dabelsteen (1996) suggested that singing quietly may be beneficial because it limits eavesdropping (e.g., from rivals, females, or predators) (but see Searcy and Nowicki 2006). Male corncrakes frequently visit territories of their neighbors and remain silent most of that time (Schäffer 1999; Skliba and Fuchs 2004). We noted many such males because they sometimes responded to playback and attacked the speaker. Aggressive responses of such eavesdropping males are unexpected, and it seems they increase the average risk of retaliation. We think that the low amplitude of soft calls could markedly decrease the number of eavesdroppers and unintended attacks and thus decrease receiver-dependent costs of signaling.

To sum up, soft calls produced by male corncrakes during antagonistic interactions are aggressive signals that appear to play a role equivalent to that of soft songs in songbirds. The similar effectiveness in eliciting an aggressive response from the receiver and in causing the receiver to retreat makes a strong case that the reliability of soft calls in the corncrake is maintained through a receiver-retaliation rule.

FUNDING

Ministry of Science and Higher Education (grant no. N N303 423836).

We thank M. Budka for his assistance in the fieldwork. The study was conducted thanks to permission given by Director of Biebrza National Park.

REFERENCES

Anderson RC, Nowicki S, Searcy WA. 2007. Soft song in song sparrows: response of males and females to an enigmatic signal. Behav Ecol Sociobiol. 61:1267–1274.

Anderson RC, Searcy WA, Peters S, Nowicki S. 2008. Soft song in song sparrows: acoustic structure and implications for signal function. Ethology. 114:662–676.

Ballentine B, Searcy WA, Nowicki S. 2008. Reliable aggressive signalling in swamp sparrows. Anim Behav. 75:693–703.

Burt JM, Campbell SE, Beecher MD. 2001. Song type matching as threat: a test using interactive playback. Anim Behav. 62:1163–1170.

Chappell MA, Zuk M, Kwan TH, Johnsen TS. 1995. Energy cost of an avian vocal display: crowing in red junglefowl. Anim Behav. 49: 255–257.

Cramp S, Simmons KEL. 1980. Birds of the Western Palearctic. Oxford: Oxford University Press.

Dabelsteen T, McGregor PK, Lampe HM, Langmore NE, Holland J. 1998. Quiet song in song birds: an overlooked phenomenon. Bioacoustics. 9:89–105.

Dabelsteen T, Pedersen SB. 1988. Song parts adapted to function both at long and short ranges may communicate information about the species to female blackbirds *Turdus merula*. Ornis Scand. 19: 195–198.

Dabelsteen T, Pedersen SB. 1990. Song information about aggressive responses of blackbirds, Turdus merula: evidence from interactive playback experiments with territory owners. Anim Behav. 40: 1158–1168.
De Kort SR, Eldermire ERB, Cramer ERA, Vehrencamp SL. 2009. The deterrent effect of bird song in territory defense. Behav Ecol. 20: 200–206.
Enquist M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. Anim Behav. 33:1152–1161.
Fitch TW, Hauser MD. 2003. Unpacking "honesty": vertebrate vocal production and the evolution of acoustic signals. In: Simmons A, Fay RR, Popper AN, editors. Acoustic communication. New York: Springer. p. 65–137.
Grafen A. 1990. Biological signals as handicaps. J Theor Biol. 144: 517–546.
Hof D, Hazlett N. 2010. Low-amplitude song predicts attack in a North American wood warbler. Anim Behav. 80:821–828.
Horn AG, Leonard ML, Weary DM. 1995. Oxygen consumption during crowing by roosters: talk is cheap. Anim Behav. 50: 1171–1175.
Hurd PL. 1997. Is signalling of fighting ability costlier for weaker individuals? J Theor Biol. 184:83–88.
Laidre ME, Vehrencamp SL. 2008. Is bird song a reliable signal of aggressive intent? Behav Ecol Sociobiol. 62:1207–1211.
Lampe HM. 1991. The response of male redwings *Turdus iliacus* to playback of conspecific songs with or without the terminating twitter. Ornis Scand. 22:137–142.
Maynard Smith J. 1979. Game theory and the evolution of behaviour. Proc R Soc Lond B Biol Sci. 205:475–488.
Maynard Smith J, Harper D. 2003. Animal signals. 1st ed. New York: Oxford University Press.
McGregor PK, Dabelsteen T. 1996. Communication networks. In: Kroodsma DE, Miller EH, editors. Ecology and evolution of acoustic communication in birds. editors. Ithaca (NY): Cornell University Press. p. 409–425.
Mennill DJ, Ratcliffe LM. 2004. Overlapping and matching in the song contests of black-capped chickadees. Anim Behav. 67:441–450.
Molles LE, Vehrencamp SL. 2001. Songbird cheaters pay a retaliation cost: evidence for auditory conventional signals. Proc R Soc Lond B Biol Sci. 268:2013–2019.
Morton ES. 2000. An evolutionary view of the origins and functions of avian vocal communication. Jpn J Ornithol. 49:69–78.
Naguib M, Wiley RH. 2001. Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. Anim Behav. 62:825–837.
Peake TM, McGregor PK. 1999. Geographical variation in the vocalisation of the corncrake *Crex crex*. Ethol Ecol Evol. 11:123–137.
Peake TM, McGregor PK, Smith KW, Tyler G, Gilbert G, Green RE. 1998. Individuality in Corncrake *Crex crex* vocalizations. Ibis. 140: 120–127.
Popp JW. 1987. Risk and effectiveness in the use of agonistic displays by American goldfinches. Behaviour. 103:141–156.
Ręk P, Osiejuk TS. 2010. Sophistication and simplicity: conventional communication in a rudimentary system. Behav Ecol. 21: 1203–1210.
Schäffer N. 1999. Habitatwahl und Partnerschaftssystem von Tüpfelralle *Porzana porzana* und Wachtelkönig *Crex crex*. Ökologie der Vögel. 21:1–267.
Schäffer N, Koffijberg K. 2004. *Crex crex* Corncrake. BWP Update. 6: 55–76.
Schäffer N, Salzer U, Wend D. 1997. Das Lautrepertoire des Wachtelkönings *Crex crex*. Vogelwelt. 118:147–156.
Searcy WA, Anderson RC, Nowicki S. 2006. Bird song as a signal of aggressive intent. Behav Ecol Sociobiol. 60:234–241.
Searcy WA, Anderson RC, Nowicki S. 2008. Is bird song a reliable signal of aggressive intent? A reply. Behav Ecol Sociobiol. 62: 1213–1216.
Searcy WA, Beecher MD. 2009. Song as an aggressive signal in songbirds. Anim Behav. 78:1281–1292.
Searcy WA, Nowicki S. 2005. The evolution of animal communication: reliability and deception in signaling systems. Princeton (NJ): Princeton University Press.
Searcy WA, Nowicki S. 2006. Signal interception and the use of soft song in aggressive interactions. Ethology. 112:865–872.
Skliba J, Fuchs R. 2004. Male Corncrakes *Crex crex* extend their home ranges by visiting the territories of neighbouring males. Bird Study. 51:113–118.
Specht R. 2007. Avisoft-SASLab Pro. Version 4.52. Berlin (Germany): Avisoft Bioacoustics.
Vehrencamp SL. 2000. Handicap, index, and conventional signal elements of bird song. In: Espmark Y, Amundsen T, Rosenqvist G, editors. Animal signals: signalling and signal design in animal communication. editors. Trondheim (Norway): Tapir Academic Press. p. 277–300.
Vehrencamp SL. 2001. Is song-type matching a conventional signal of aggressive intentions? Proc R Soc Lond B Biol Sci. 268:1637–1642.
Vehrencamp SL, Hall ML, Bohman ER, Depeine CD, Dalziell AH. 2007. Song matching, overlapping, and switching in the banded wren: the sender's perspective. Behav Ecol. 18:849–859.
Zahavi A. 1977. The cost of honesty (further remarks on the handicap principle). J Theor Biol. 67:603–605.