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Title: The function of three main call types in common cuckoo

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Abstract: Acoustic signals play a key role in shaping the relationships in birds. Common cuckoos *Cuculus canorus* are known to produce various call types, but the function of these calls has only been studied recently. Here, we used a combination of field recordings (conducted in 2017) and playback experiments (conducted in 2018) to investigate the functional significance of common cuckoo calls. We found significant differences in the characteristics between male two-element ‘*cu-coo*’ and three-element ‘*cu-cu-coo*’ calls, with these two call types being used in different contexts. The three-element male ‘*cu-cu-coo*’ calls were associated with females emitting their ‘bubbling’ call. Playback experiments revealed that both males and females exhibit stronger responses to playing female “bubbling” calls than with the calls of Eurasian sparrowhawk (*Accipter nisus*) serving as a control suggesting a significant intraspecific communication function for this call type. However, we did not find any evidence to support mate attraction in male calls, as females were not stimulated by playback of male calls compared to sparrowhawk calls in the control group.

Key words: acoustic signals; China; common cuckoo; female vocalization; playback; sparrowhawk.

Introduction

Relationships among individuals are adjusted by the transmission of signals (Boughman, 2002; Hurd & Enquist, 2005; Partan, 2013). There are several channels for signal transmission, such as acoustic, visual, chemical and tactile (Partan, 2013; Rubi & Stephens, 2016). Among these channels, acoustic signals can take effect in darkness, penetrate through objects, and can be transmitted over long distances (Lemon, 1977; Slabbekoorn & Smith, 2002). Therefore, not surprisingly, acoustic signals play a key role in adjusting relationships in birds (Todt & Naguib, 2000; Slater, 2003). Passeriformes adopt versatile vocations to attract a partner and/or deter rivals (Catchpole & Slater, 2008). In non-Passeriformes, vocalizations are often simple and stereotyped, but messages can also be encoded in different call types. For examples, adult African penguin (*Spheniscus demersus*) employ four vocal categories for use in different circumstances (Favaro et al., 2014); male corncrakes (*Crex crex*) are known to express low or high levels of aggressive motivation in broadcast calls and soft calls, respectively (Rek & Osiejuk, 2011); and male ural owls (*Strix uralensis*) use different call types for territorial advertisement and for duetting with female (Lundberg, 1980).

For cuckoos, a well-studied brood parasitic avian species, the temporal and frequency variables of male 'cu-coo' calls (Fig. 1a) are well-known (Lei et al., 2005). This call type is sufficient to provide individual information (Jung et al., 2014; Li et al., 2017; Zsebok et al., 2017), which can be used to distinguish between neighbors and strangers (Moskát et al., 2017, 2018): male cuckoos show less aggressive response to familiar '*cu-coo*' calls from neighbors than unfamiliar '*cu-coo*' calls from strangers during playback experiments. Besides the characteristic and conspicuous two-element '*cu-coo*' calls, males can also utter a three-element '*cu-cu-coo*' call (Fig. 1b) which contains a repeat of the first element of the regular '*cu-coo*' call (Lei et al., 2005; Payne, 2005). Based on our experience and previous research (e.g. Lei et al., 2005), '*cu-coo*' calls can be heard very often at our study site, but '*cu-cu-coo*' calls are much rarer. The exact function of this three-element call is unknown but is thought to be associated with female activity (Payne, 2005; Erritzøe et al., 2012; Tryjanowsi et al., 2018), however empirical evidence for this is scant. Different cuckoo calls have also been a common component of folklore (Møller et al., 2017), suggesting that not only cuckoos, but also humans respond to differences in cuckoo calls.

Female cuckoos give a conspicuous 'bubbling' (or 'chuckle') call (Fig. 1c) (Lei et al., 2005; Payne, 2005). One recent study suggested that these 'bubbling' calls mimic those of the Eurasian sparrowhawk (*Accipter nisus*), serving primarily as a distraction of host species after laying (York & Davies, 2017). However, a more recent study has suggested that female cuckoo calls may have other functions besides distraction of nest hosts (Deng et al., 2019), as female cuckoos predominantly lay their eggs in the afternoon (Payne, 2005; Erritzøe et al., 2012), but vocal activity of female 'bubbling' calls peak in the morning, with nearly no call output in the afternoon (Deng et al., 2019). Besides, Benedetti et al. (2018) found the number of syllables in male cuckoos call was negatively correlated with the presence of female 'bubbling' calls, which implies intraspecific communication function of the female 'bubbling' calls.

In this study, we investigate the function of three cuckoo call types using a series of playback experiments and new field recordings of both male and female calls. Our first aim was to quantify the features of the three-element male ‘*cu-cu-coo*’ call, and to determine whether this call was associated with female activity. The second aim was to investigate the intersexual function of the male two-element ‘*cu-coo*’ calls using playback of male calls to female cuckoos. The function of the male ‘*cu-coo*’ call is assumed to deter territorial rivals and attract mates (Payne, 2005). Deterring territorial rivals has been repeatedly demonstrated in previous cuckoo studies (Moskát et al., 2017, 2018; Tryjanowski et al., 2018). However, empirical field tests concerning the function of attracting females is still in its infancy. We predicted that females were attracted by male calls. Our third and final aim was to determine the intraspecific communication function of the female ‘bubbling’ calls using playback trials of this call type to both male and female cuckoos. We predicted that if there is an intraspecific effect in this call type, then we would detect ~~a~~ significant behavioral changes after playback of this call type.

Methods

Study area

Fieldwork was conducted during the breeding season (May to July) in 2017 and 2018 at the Liaohe Delta Nature Reserve (41.034°N; 121.725°E), Liaoning Province, Northeast China. This region has a semiarid continental monsoon climate with rainfall usually occurring from July to September, and it represents one of the most important estuarine wetlands, with the largest area of reed-bed habitat (about 800 km^2) along the coastal region of China. Due to oil fields in the wetlands, energy projects are being constructed. The oil field infrastructures have resulted in installation of electrical wires, which provide perch sites for the cuckoos. Here, the common cuckoo is a summer breeding species, and it predominantly parasitizes Oriental reed warbler

(*Acrocephalus orientalis*) nests (Li et al., 2016). The breeding season for the common cuckoo lasts from May to July in this area, and typically the first individual cuckoos are seen around the middle May, and the last Oriental reed warbler nests found around late July each year (Li et al., 2016).

Sound recording

We used a recorder (DR-100MKIII, Tascam Co., Japan) and an external directional microphone (MKH416 P48, Sennheiser Co., Germany), with a sampling rate of 44.1 kHz and a sampling accuracy of 16 bits, to record cuckoo vocalizations. Further recordings were made using seven passive acoustic recorders (SM4, Wildlife Acoustics Inc., USA) placed at seven different locations, separated by a minimal distance of 200 m, to continuously record cuckoo calls from June 8th to July 28th 2017. Recorders were attached to telegraph poles at a height of 3 m above ground, and set to record continuously at a sampling rate of 44.1 kHz, and a sampling accuracy of 16 bits. Recorders were checked every 10 days to replace the batteries and memory cards. In addition, we used mist nets to trap and band 20 individual adult common cuckoos (6 females and 14 males) around our recording sites, whilst daily observations also revealed the presence of many other unbanded individual cuckoos at these same locations during data collection. These 20 individuals were banded with metal rings and backpack radio transmitters (weight 2.12g, Biotrack, UK).

Sound measurements

All recordings were re-sampled with 6 kHz, and saved as .wav files. We used Avisoft-SASLab Pro 5.2 audio analysis software (Avisoft Bioacoustics, Germany) to generate spectrograms with the following settings: fast Fourier transform length 256 points; Hamming window with a frame size of 100% and an overlap of 50%; frequency resolution 23 Hz; and time resolution of 21 ms. By checking the spectrograms, we found a total of 24 three-element ‘*cu-cu-coo*’ calls recorded from 11 banded males: 3

‘*cu-cu-coo*’ calls were recorded in 3 males, 2 ‘*cu-cu-coo’* calls were recorded in 7 males, and one ‘*cu-cu-coo*’ call was recorded in one male. We measured four variables for each ‘*cu-cu-coo’* call: duration, minimum frequency, maximum frequency, and peak frequency (frequency of the maximum amplitude). We also measured 24 ‘*cu-coo*’ calls from the same 11 banded males, all of which were recorded immediately before or after the ‘*cu-cu-coo*’ calls. For these calls, we measured the same four variables: duration, minimum frequency, maximum frequency, and peak frequency.

In order to determine whether male ‘*cu-cu-coo*’ calls are associated with female activity (emitting ‘bubbling’ call), we compare the number of two-element ‘*cu-coo*’ and three-element ‘*cu-cu-coo*’ calls 30 s before or after female ‘bubbling’ calls. Firstly, we used Kaleidoscope Pro software (Wildlife Acoustics Inc., USA) to create recognizers for identifying all female ‘bubbling’ calls from recordings collected with seven passive acoustic recorders. We entered the following acoustic features to Kaleidoscope Pro Software: frequency range from 600 to 2900 Hz; duration ranges from 1.6 to 4 s. These acoustic features are slightly larger than actual parameters of female ‘bubbling’ calls, but this was done simply to increase the detectability of these calls by the Kaleidoscope Pro Software. Then, we manually checked all calls identified by the recognizer based on visual inspection of the spectrograms, resulting in 2,407 female ‘bubbling’ calls. Next, we selected all female ‘bubbling’ call bouts which were separated by a minimum interval of 30 mins with other female call bouts, to ensure male calls are affected by the target ‘bubbling’ call, rather than adjacent ‘bubbling’ call, resulting in 144 ‘bubbling’ calls for subsequent analyses. Lastly, we manually counted the number of ‘*cu-coo*’ and ‘*cu-cu-coo*’ calls 30 s before or after female ‘bubbling’ calls from spectrograms. We were unable to automatically detect male calls using Kaleidoscope Pro Software due to the difficulty in distinguishing between the three-element and two-element calls which may be attributed to the shared ‘*cu*’ and ‘*coo*’ elements in both types of calls.

Playback experiments

Playback experiments were conducted in two periods defined here as the early breeding season (28th May to 8th June) and late breeding season (5th to 28th July) in 2018. We used 12 sound files belonging to 4 call types (i.e.3 sound files in each call type): two-element male ‘*cu-coo*’ calls (Fig. 1a), three-element male ‘*cu-cu-coo*’ calls (Fig. 1b), female ‘*bubbling*’ calls (Fig. 1c), and Eurasian sparrowhawk calls (Fig. 1d) to act as a control. The Eurasian sparrowhawk is an uncommon predator of small songbirds in the study area, but there are no reports of it being a threat to adult common cuckoos. Each sound file lasted 2 min. The basic elements of a sound file contained some repeated bouts from the same individual, composing a 30 s unit, followed by a 15 s break. This set was repeated, and then the whole 30 s sound unit was added to complete the playback sound file. The duration of different bouts varied so we also varied the number of bouts (from 3 to 9 bouts) in each 30 s unit of the different sound files, whilst ensuring that the proportion of total calls duration in 30 s units were uniform in all sound files. Subsequently each sound file was edited using Goldwave 5.25 (GoldWave Inc., Canada). To avoid pseudoreplication, we used calls from different individuals to create different sound files. Cuckoos calls were recorded during the 2017 breeding season in the study area, and sparrowhawk calls were downloaded from Xeno-Canto (http://www.xeno-canto.org, ID XC107015, ID XC120729, ID XC143459, recorded in Kyrgyzstan and Poland), a non-profit website set up to share recordings of sounds of wild birds.

For playbacks, we used a smartphone player (Honor 8; Huawei Technologies Co., China) connected to a loudspeaker (SME-AFS; Saul Mineroff Electronics Inc., USA), with the playback amplitude set to normal call amplitude of cuckoos, approximately 95 dB SPL measured at 1 m with a sound level meter (NL-20; Rion Co., Japan). All trials were conducted between 0700 and 1900 h, after the end of the dawn chorus and before the peak of the dusk chorus. Playback experiments were started in the close vicinity of cuckoos observed. The loudspeaker was positioned about 20 m from the observers, about 68 ± 10 m (mean ± SD, range 39 to 95 m) from the target cuckoo, which always perched on electrical wires. As most target cuckoos for our trials were not banded, we conducted playback experiments targeting individuals separated by at least 1 km to try our best to avoid repeated sampling from the same individual in each period (either early breeding season or late breeding season). Each target cuckoo was only used once in each period, played with one randomly selected sound file.

Following the method used by Moskát et al. (2017, 2018), we measured the following four variables during the playback experiments: starting distance (distance between the focal cuckoo and the loudspeaker at the beginning of playback); closest distance (the distance of closest approach to the loudspeaker during 2 min playback); movement latency (when the focal cuckoo moved from its original position at the start of the playback); and sound latency (when the focal cuckoo started calling). Starting distance and closest distance were measured with a range finder (ELITE 1500; Bushnell Corp. USA). Movement latency and sound latency were measured with a stopwatch (Tianfu PC396; Shenzhen Huibo Industry & Trade Co., China). If a target individual cuckoo did not move or call during 2 minutes of playback, movement latency or sound latency was recorded as 120 s. If an individual cuckoo did not call during playback, we continued observations until it called, and recorded the sex based on the call type (males utter '*cu-coo*' or '*cu-cu-coo*' calls, while females utter 'bubbling' calls). We discarded 6 playback trials from subsequent analyses due to fighting between cuckoos (3 occasions), or because the target individual was chased by Oriental reed warblers (2 occasions), or they flew away in response to passing vehicles (1 occasion) during the playback trail. Overall, we successfully conducted playback experiments to 74 individuals during early breeding season, and 58 individuals in late breeding season. Cuckoos calls used in the playback experiments were collected in the same area occupied by the focal individual cuckoos, so there is a possibility that these calls were from neighboring individuals to the focal cuckoos. In addition, focal cuckoos may show specific response to these familiar calls, however, the large sample sizes obtained in this study can minimize the chance of such cases.

Data analyses

We measured four variables: duration, minimum frequency, maximum frequency, and peak frequency for both the two-element *'cu-coo'* call and three-element *'cu-cu-coo'* calls. When comparing these call variables, four linear mixed models were used. In each model, one of the call variables was the response variable, with male call type (*'cu-coo'* or *'cu-cu-coo'*) as the fixed effect and bird ID as the random effect. For comparing the number of two-element and three-element male calls 30 s before or after a female call, we used the number of '*cu-coo*' and '*cu-cu-coo*' calls as the response variable in each model, with period (30 s before or after female 'bubbling' calls) as the fixed effect, and recorder ID as the random effect.

Following the method used by Moskát et al. (2017, 2018), we used distance difference (starting distance minus closest distance), movement latency, and sound latency to reflect the degree of excitement during playback. Since these three variables are highly correlated (KMO and Bartlett's test, KMO value = 0.71, $P <$ 0.001), we applied principal component analysis and used the first principal component with eigenvalue = 2.25 to reflect the original variables. Playback experiment data were then divided into four data sets based on the sex of target cuckoos and period: males in early breeding season, males in late breeding season, female in early breeding season, female in late breeding season. We used four linear mixed models for these four data sets, with the first principal component entered as the response variable, sound type used in playback, date of the playback experiment and time as fixed effects (due to the fact that bird activity may be influenced by breeding condition and daily activity), and the ID of the sound file as the random effect.

Considering that censored data were used for measuring behavior during playback experiments, e.g. a target individual cuckoo did not move or call during 2 min playback, movement latency or sound latency was recorded as 120 s. We also employed Mann-Whitney test to analyze playback experiment data: comparing the responses among different groups. Mann-Whitney test based on ranks rather than original values is generally less sensitive to censored data. The results are quite similar to the results in the linear mixed models described above, and presented in Appendix 1.

All analyses were performed using R software (R Core Development Team, 2018), with the linear mixed model conducted in package *lme4* (Douglas et al., 2015). Data are presented as mean ± SD and P values less than 0.05 were considered statistically significant.

Results

Our recordings revealed that the structure of the two-element ‘*cu-coo*’ and three-element ‘*cu-cu-coo*’ calls were similar (Fig. 1a and b). However, three-element calls were of significantly longer duration and had significantly higher minimum, maximum and peak frequency (Table 1). Output from the linear mixed models revealed that the two call types were used in different contexts. There were significantly less ($t_{280} = 2.03$, $P = 0.044$) two-element male ‘*cu-coo*’ calls emitted after (3.68 ± 4.93) than before (5.10 ± 6.81) female calls, while there was a significantly greater ($t_{280} = 3.96$, $P < 0.001$) number of three-element male ‘*cu-cu-coo*’ calls emitted following female calls (1.12 ± 1.59) than before (0.49 ± 1.09; Fig. 2).

The three observed variables in playback experiments are highly correlated (KMO and Bartlett's test, KMO value = 0.71, $P < 0.001$). Therefore, we applied principal component analysis and used the first principal component, with eigenvalue = 2.25 explaining 74.9 % of the variance in the original variables, as a measure of the degree of activity. This principal component was positively related to the difference in distance (correlation coefficient = 0.84), and negatively related to both movement latency (correlation coefficient = -0.90) and sound latency (correlation coefficient = -0.86). Thus, we named the principal component ‘excitement’, with large values indicating a high degree of activity (i.e. approach the loudspeaker, fly early, call early) during playback.

Playback experiments revealed that males show higher degree of excitement in response to the playback of female ‘bubbling’ calls than those of the control (playing sparrowhawk calls) during both the early breeding season and late breeding season (Fig. 3, Table 2). Males exhibited a higher degree of excitement to male two-element ‘*cu-coo*’ calls during playback, than toward the sparrowhawk calls but only during the early breeding season (Fig. 3, Table 2). In response to playback of the three-element male ‘*cu-cu-coo*’ calls, males did not show a significant difference compared to playback of the sparrowhawk calls either during the early or late breeding season (Fig. 3, Table 2). In contrast, females exhibited a higher degree of excitement in response to playback of female ‘bubbling’ calls than the controls during both early and late breeding season (Fig. 4, Table 3). Females did not show a significant difference in response to both types of male calls when compared to sparrowhawk calls in either the early breeding season or late breeding season (Fig. 4, Table 3).

Discussion

Is the male ‘*cu-cu-coo*’ call associated with female activity?

Despite the three-element calls having previously been quantitatively described by Lei et al. (2005), this call type has been omitted as abnormal calls in other studies (e.g. Wei et al., 2015). Historically this three-element call type was considered to be associated with female ‘bubbling’ calls (Payne, 2005; Lei et al., 2005), but there has been no empirical study to support this suggestion. In this study we compared the number of calls emitted 30 s before or after a female ‘bubbling’ call which we found was the only call type that stimulated males during both early and late breeding season amongst the call types tested. We found that the number of male three-element ‘*cu-cu-coo*’ calls increased significantly following the female ‘bubbling’ call while the number of two-element male ’*cu-coo*’ calls decreased. Our findings support the idea that the three-element male ‘*cu-cu-coo*’ call is associated with females emitting ‘bubbling’ calls. In addition, we found that the three-element ‘*cu-cu-coo*’ call is significantly longer in duration and with higher frequency, compared with the two-element ‘*cu-coo*’ call. In some Passeriformes species, long and higher frequency song types are associated with sexual selection (Gil et al., 2007; Cardoso, 2012; Nelson & Poesel, 2012) and are more efficient in attracting a mate. It could be that male common cuckoos also adopt this tactic.

Is the function of the male call to attract females?

In non-Passeriformes, vocalizations are often simple and stereotyped, with no song behavior (Catchpole & Slater, 2008). However, some non-Passeriformes, such as cuckoos (*Cuculus* spp.), utilize a song that, although stereotyped, is important during the breeding season (Kroodsma & Miller, 1996). Call features always served as an important basis for interspecies classification in different cuckoo species (Xia et al., 2016; Kim et al., 2017). Although it is tacitly assumed that cuckoo vocalizations during the breeding season serve as a means of mate attraction (King, 2005; Xia, et al. 2016), this crucial assumption remains untested empirically. In this study we did not find any evidence that females were stimulated by playback of male calls compared to the control playback of sparrowhawk calls. Interestingly, we did find an association between the three-element male '*cu-cu-coo*' call and female 'bubbling' call. However, the female did not show a higher degree of excitement in response to playback of the three-element '*cu-cu-coo*' call, and, consequently, did not find any evidence to support the suggestion that the function of the male call is to attract females. However, we could not rule out a female response in some subtle ways, e.g. change in posture and heart rate during playback. Even in Passeriformes, direct evidence for a mate attraction function in male song is far less abundant (Kroodsma & Byers, 1991). The majority of studies supporting the mate attraction function has been collated from laboratory-based studies, with contradictory observations about mate attraction by male song from field-based studies (Byers & Kroodsma, 2009; Soma & Garamszegi, 2011). For common cuckoos, whether male calls function to attract females remains an open question.

The function of the female 'bubbling' call

Historically, most attention to variation in avian vocal signals has been directed towards males (Beecher & Brenowitz, 2005). However, female vocalizations are also widespread in birds (Garamszegi et al., 2007; Yang et al., 2011; Odom et al., 2014) e.g. female song sparrows (*Melospiza melodia*) sing during territorial conflicts with other females (Arcese et al., 1988), and female blue tits (*Cyanistes caeruleus*) are known to sing when their nests are approached by sparrowhawks (Mahr et al., 2016). One recent experimental playback study has suggested that the female cuckoo bubbling call primarily serves as a distraction of the host parent species (York and Davies, 2017). Such a function would enable female cuckoos to benefit from reducing their egg rejection rate through distraction of the attention of hosts (York & Davies, 2017). Based on playback experiments in this study, clearly common cuckoos are able to distinguish between female 'bubbling' calls and that of the sparrowhawk since both male and female common cuckoos show higher degree of excitement in response to playback of the female call. Despite this, the female ‘bubbling’ call may mean different things to the two sexes. During daily observations, we found that males often flew with females after a female called. Thus, female calls may function as a signal to attract males. For females, the ‘bubbling’ call may function as a signal to defend resources e.g. host nests. Similar phenomena have also been discovered in a recent research (Moskát & Hauber, 2019). Based on these findings, and those of our previous research, which found that vocal activity of female common cuckoos in the same study population peaked in the morning (Deng et al., 2019), we suggest that the primary function of the female ‘bubbling’ call in this population is intraspecific communication, rather than distraction of nest hosts.

Conclusion

In this study, we used call recordings and playback experiments to determine the function of different common cuckoo call types. Firstly, we demonstrated that the three-element male ‘*cu-cu-coo*’ call is associated with the female ‘bubbling’ call. Secondly, we did not find clear evidence supporting the proposed function of mate attraction in male calls. Finally, we suggest that intraspecific communication is the primary function of the female ‘bubbling’ call in our study population, as both male and female common cuckoos show higher degree of excitement in response to playback of female calls.

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Table 1. Call features (mean ± SD) of 24 ‘*cu-coo*’ calls and 24 ‘*cu-cu-coo*’ calls from 11 individual cuckoos. Call features were compared using linear mixed models, with individual ID as the random effect.

Call features	‘*cu-coo*’ call	‘*cu-cu-coo*’ call	t value	*P*
Duration (s)	0.43 ± 0.04	0.62 ± 0.05	17.12	< 0.001
Minimum frequency (kHz)	0.62 ± 0.03	0.66 ± 0.03	5.98	< 0.001
Maximum frequency (kHz)	1.01 ± 0.06	1.18 ± 0.08	8.45	< 0.001
Peak frequency (kHz)	0.83 ± 0.12	0.94 ± 0.13	12.81	< 0.001

Table 2. Male cuckoos responded differently to playback of different call types. Playback of sparrowhawk calls was used as a control.

Variables	Early breeding season			Late breeding season		
	Coefficient ± SE	t	*P*	Coefficient ± SE	t	*P*
Playback male ‘*cu-coo*’ calls	1.59 ± 0.36	4.37	0.002	0.68 ± 0.4	1.71	0.126
Playback male ‘*cu-cu-coo*’ calls	0.7 ± 0.37	1.91	0.092	-0.09 ± 0.42	-0.21	0.842
Playback female ‘bubbling’ calls	1.81 ± 0.36	5.09	0.001	1.42 ± 0.38	3.78	0.005
Time	-0.3 ± 0.58	-0.51	0.612	-2.51 ± 1.34	-1.88	0.073
Date	-0.06 ± 0.03	-2.14	0.040	-0.01 ± 0.02	-0.50	0.625

Table 3. Female cuckoos responded differently to playback of different call types. Playback of sparrowhawk calls was used as a control.

Variables	Early breeding season			Late breeding season		
	Coefficient ± SE	t	*P*	Coefficient ± SE	t	*P*
Playback male ‘*cu-coo*’ calls	-0.32 ± 0.5	-0.63	0.555	0.03 ± 0.54	0.06	0.951
Playback male ‘*cu-cu-coo*’ calls	-0.18 ± 0.48	-0.38	0.723	0.39 ± 0.55	0.72	0.490
Playback female ‘bubbling’ calls	1.44 ± 0.47	3.06	0.028	1.56 ± 0.52	3.00	0.017
Time	-0.17 ± 1.16	-0.14	0.888	0.27 ± 1.9	0.14	0.893
Date	-0.06 ± 0.05	-1.21	0.244	0 ± 0.03	-0.15	0.884

Figure legends:

Figure 1. Spectrogram of male common cuckoo ‘*cu-coo*’ call (a); male common cuckoo ‘*cu-cu-coo*’ call (b); female common cuckoo ‘bubbling’ call (c); and sparrowhawk call (d).

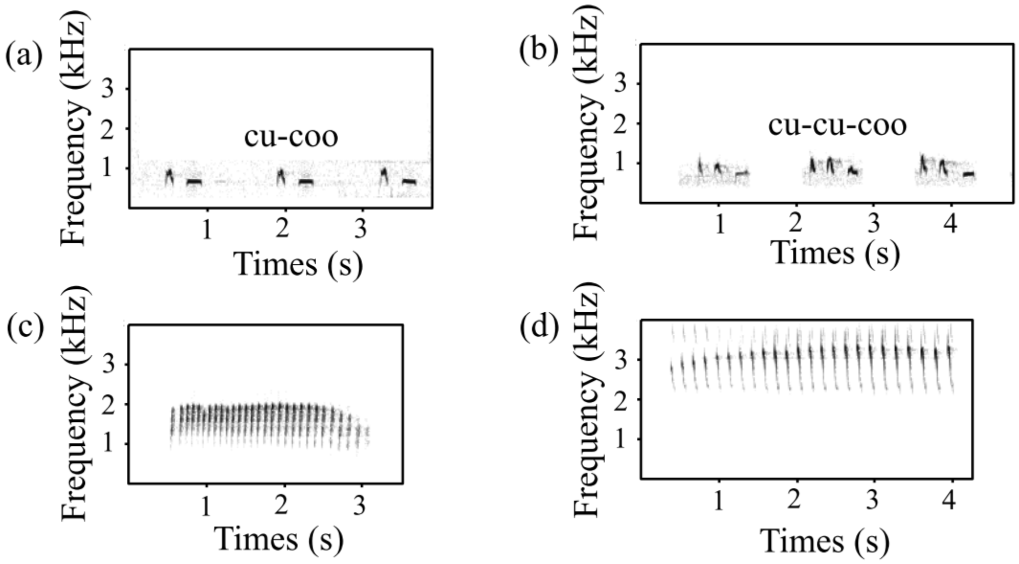


Figure 2. Comparison of the number of male ‘*cu-coo*’ and ‘*cu-cu-coo*’ calls recorded 30 s before or after playback of female ‘bubbling’ calls. Asterisk indicates significant difference based on linear mixed models, with recorder ID as the random effect.

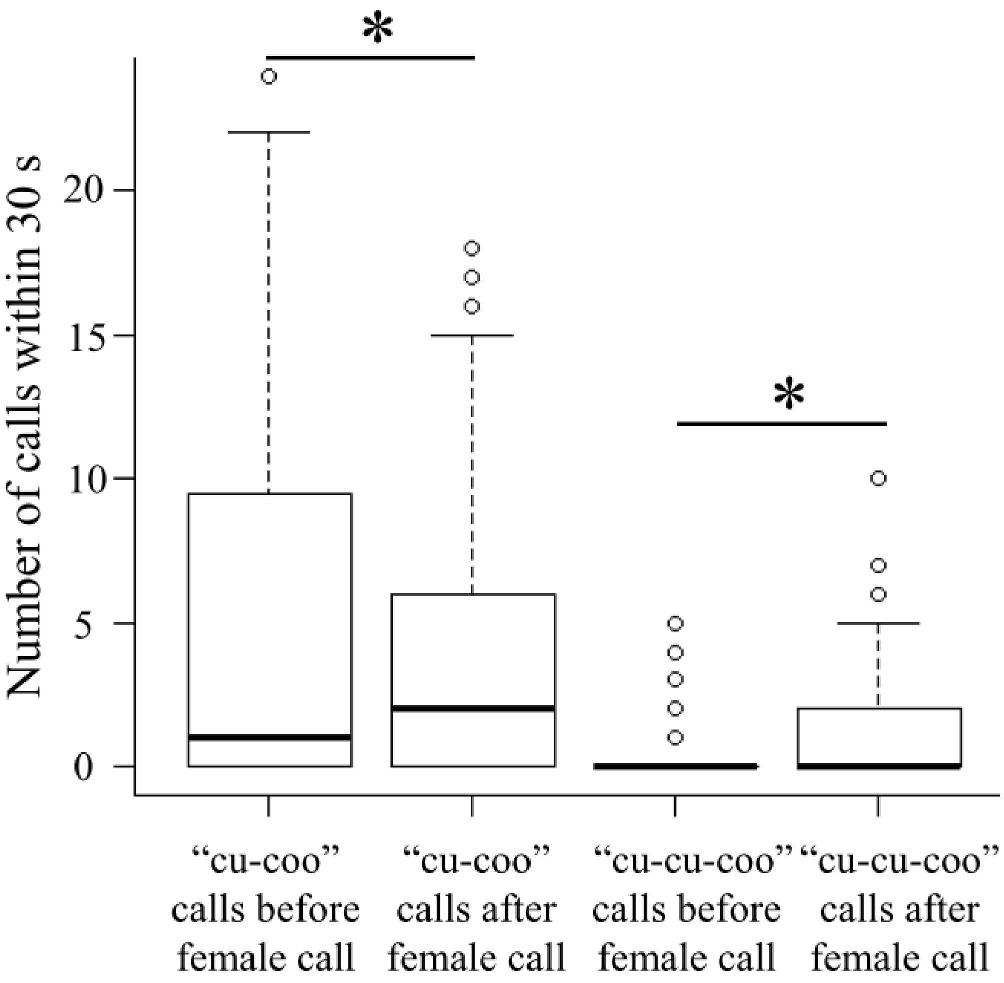


Figure 3. Response of male common cuckoos to playback (measured as degree of excitement). White bar indicates playback experiments in early breeding season (28th May to 8th June in 2018), while black bars indicate playback experiments in late breeding season (5th to 28th July in 2018). Sample sizes are shown above each bar. Asterisk indicates significant difference compared to control (playing sparrowhawk calls).

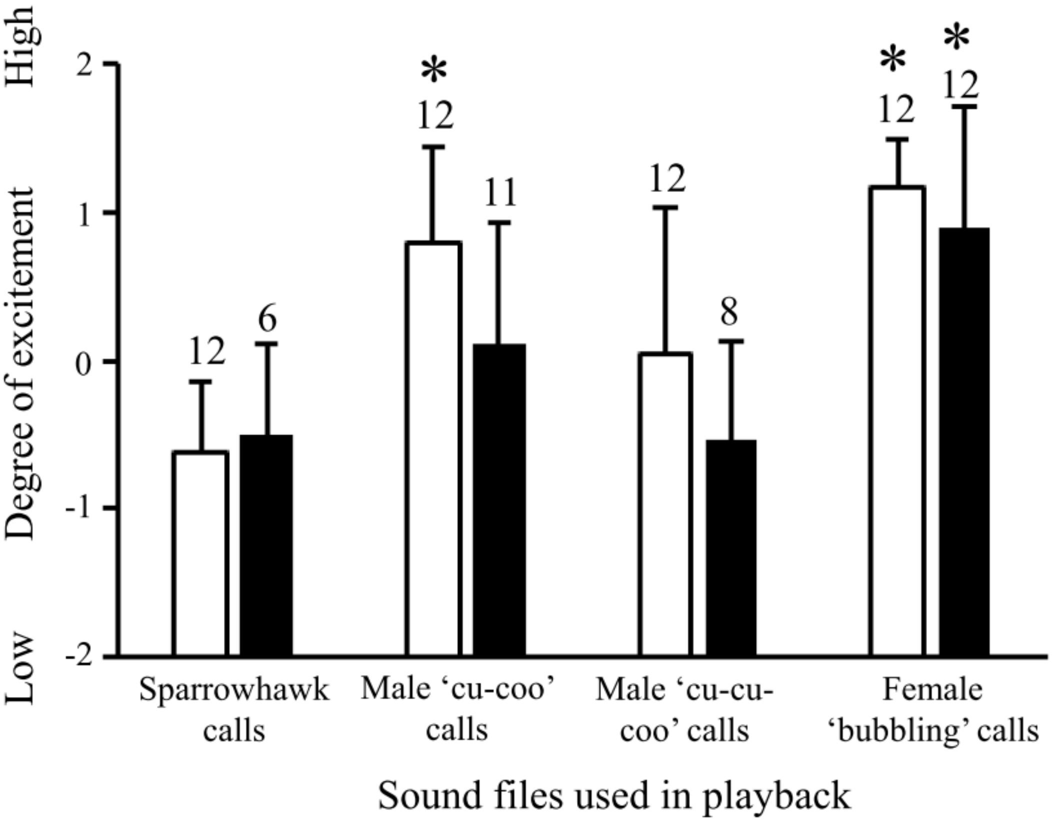
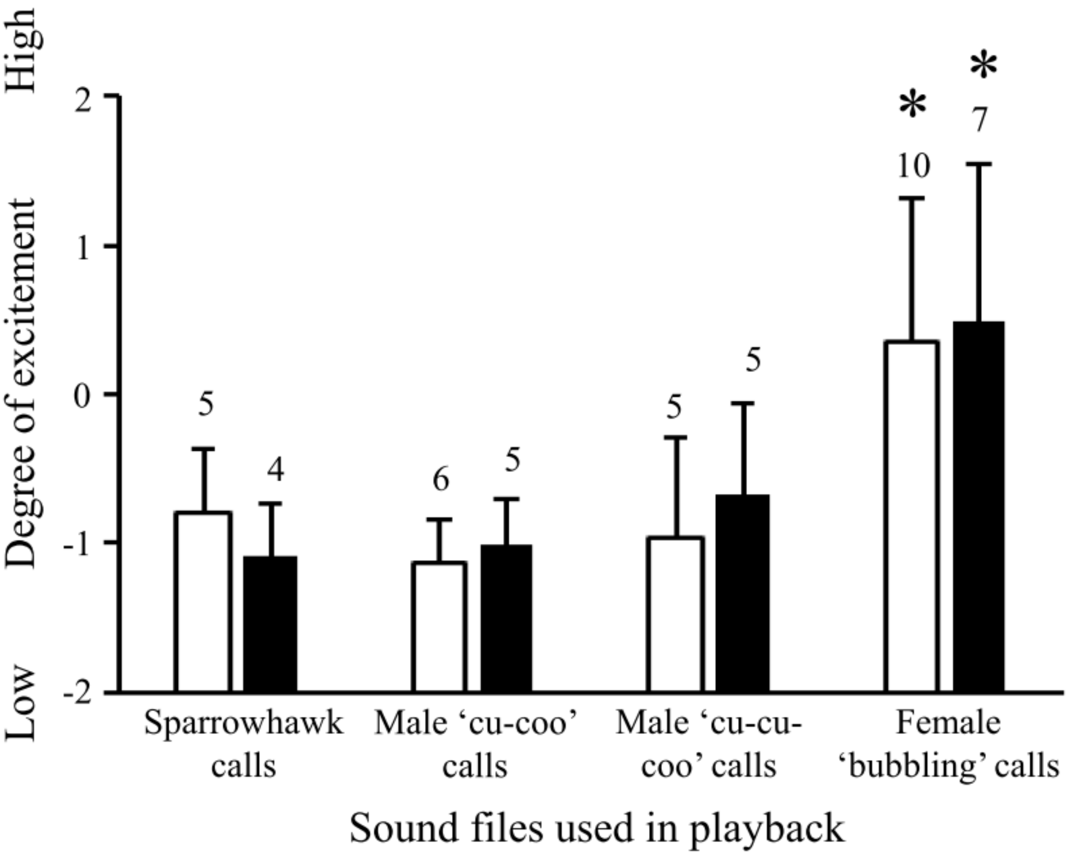


Figure 4. Response of female common cuckoos to playback (measured as degree of excitement). White bars indicate playback experiments in early breeding season (28th May to 8th June in 2018), while black bars indicate playback experiments in late breeding season (5th to 28th July in 2018). Sample sizes were shown above each bar. Asterisk indicates significant difference comparing to control (playing sparrowhawk calls).



SUPPORTING INFORMATION

Appendix 1. Cuckoos responded differently to playback of different call types. Playback of sparrowhawk calls was used as a control. Analysis is based on Mann-Whitney test.

Groups	Early breeding season				Late breeding season			
	Male		Female		Male		Female	
	Z	*P*	Z	*P*	Z	*P*	Z	*P*
Playback male ‘*cu-coo*’ calls	3.64	< 0.001	1.38	0.247	1.50	0.151	0.81	0.556
Playback male ‘*cu-cu-coo*’ calls	1.16	0.260	0.82	0.548	0.24	0.864	1.07	0.413
Playback female ‘bubbling’ calls	4.16	< 0.001	2.33	0.019	2.53	0.010	2.22	0.024