Behavioural Processes 191 (2021) 104472

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Male common cuckoos use a three-note variant of their "cu-coo" call for duetting with conspecific females

Csaba Moskát [a,*], Márk E. Hauber [b]

[a] MTA-ELTE-MTM Ecology Research Group of the Eötvös Loránd Research Network, A Joint Research Group of the Biological Institute of the Eötvös Loránd University, Pázmány P. st. 1/C, H-1117 Budapest, Hungary and the Hungarian Natural History Museum, Budapest, Hungary
[b] Department of Evolution, Ecology, and Behavior, School of Integrative Biology, University of Illinois at Urbana-Champaign, 505 S. Goodwin Avenue, Urbana, IL, 61801, USA

ARTICLE INFO

Keywords:
Brood parasite
Duetting
Pair bonding
Vocalisation

ABSTRACT

Duetting is a coordinated form of acoustic communication with participants uttering calls or songs simultaneously and/or sequentially. Duetting is often observed in pair-bonded species, with mated females and males both contributing to the communal vocal output. We observed duetting between the sexes in the common cuckoo (*Cuculus canorus*), an obligate brood parasitic species without known pair formation. Specifically, female cuckoos use their sex-specific bubbling calls for duetting, while male cuckoos use a 3-note variant ("cu-cu-coo") of their typical and well-known 2-note ("cu-coo") territorial advertisement calls. The maximum frequency of the elements in the male's 3-note variants was higher relative to the 2-note calls, while durations of both the elements and the inter-element intervals were shorter. The vast majority (95 %) of the 3-note calling was detected together with the bubbling call, implying an intersexual duetting function, with the female calls preceding these male calls in 67 % of cases. The two call types in duetting followed each other rapidly (mean response time of females was 1.30 ± 0.71 SD s, and 0.76 ± 0.53 SD s in males), and typically overlapped with each other (95 %). Frequently (90 %), the male call was repeated 2–3 times, whereas the female call was repeated less frequently (9%). Our results are consistent with a main function of duetting in intersexual communication and coordination between female and male cuckoos.

1. Introduction

Coordinated mutual calling or singing between two individuals, often between a female and a male, is called duetting and it occurs in diverse social and ecological contexts and across a broad range, including many avian lineages (Hall, 2009). Duetting indicates a high level interindividual coordination, and may imply cooperation, between sexes (Logue and Krupp, 2016). However, the function of duetting varies widely (Dahlin and Benedict, 2014), from territory defence to sex recognition, and from simple contact to mate attraction and pair bond maintenance (Thorpe, 1967; Langmore, 1998; Hall, 2004; Rogers et al., 2007), as well as mate guarding (Rogers et al., 2007). Although females and males may use a large repertoire for duetting (Hall, 2009; Sikora et al., 2021), sometimes they predominantly use a simpler set of song types. For example, the yellow-breasted boubou (*Laniarius atroflavus*) uses one male and one female song type in 81 % of its duetting (Wheeldon et al., 2020, 2021) and in a closely-related species, the crimson-breasted shrike (*Laniarius atrococcineus*), the same metric reaches 100 % (van den Heuvel et al., 2013). Duetting also occurs in non-oscine birds with non-learned vocalisations, for example in owls (Strigiforms; Delgado and Penteriani, 2007; Odom and Mennill, 2010), the water rail (*Rallus aquaticus*; Jedlikowski et al., 2021), some of the coucals (*Centropus* spp., Maurer et al., 2008; Brumm and Goymann, 2017), and a parrot (*Amazona auropalliata*; Seddon et al., 2002). It was also described for different families of African birds, including several parasitic African cuckoo species (Cuculidae; Payne, 1971).

Duetting has not been described previously in the common cuckoo (*Cuculus canorus*), a widespread obligate avian brood parasite in the Palearctic. Although the male common cuckoos' typical "cu-coo" call is well-known all over the world, the cuckoos' repertoire of vocalisations is simple (Lei et al., 2005). As cuckoos are vocal non-learners (Brenowitz, 1991; Jarvis, 2013), they cannot learn their calls' acoustic elements either from conspecifics or from host foster parents.

Male cuckoos almost continuously repeat their loud "cu-coo"

* Corresponding author.
E-mail address: moskat.csaba@nhmus.hu (C. Moskát).

https://doi.org/10.1016/j.beproc.2021.104472
Received 13 March 2021; Received in revised form 20 July 2021; Accepted 2 August 2021
Available online 5 August 2021

advertisement call during the breeding season (Lei et al., 2005; Møller et al., 2016). Regarding female cuckoos, there is only one "jack of all trades", multi-content vocalisation, the bubbling call, which is used for (i) proclaiming individual females' laying territories (Deng et al., 2019; Moskát and Hauber, 2019), (ii) dampening aggressive host responses at parasitic nest inspection and laying attempts (York and Davies, 2017; Marton et al., 2021), and (iii) in female-male communication (Moskát and Hauber, 2019). Regarding the latter function, from previous studies it seems to be evident that a variant of the 2-note "cu-coo" male call, the so-called 3-note cuckoo call ("cu-cu-coo"; Xia et al., 2019) could also be used for male-female acoustic communication in common cuckoos (Deng et al., 2019; Moskát and Hauber, 2019; Xia et al., 2019). Benedetti et al. (2018) also reported that cuckoo males changed their vocal patterns when in proximity of females. The bubbling call and 3-note call often overlap when uttered (our observations; Fig. 1).

Here we studied whether cuckoos engage in intersexual duetting by examining natural cases of communication and measuring the response latency of each sex to the other's calls. We hypothesized that male cuckoos use the 3-note cuckoo call and females use their bubbling call for duetting. We predicted that both males and females would respond rapidly to these call types of the other sex. We also evaluated the potential bioacoustic features through which the rarer variant of the cuckoo call, the 3-note call ("cu-cu-coo") could have a different function from the structurally very similar 2-note cuckoo call ("cu-coo").

2. Study area and methods

We sound-recorded cuckoo calling behaviours within a 20 × 30 km study area around the village of Apaj (47 ° 6′ 53.9″ N; 19 ° 5′ 21.2″ E), about 50 km south of Budapest, central Hungary. Here common cuckoos parasitize great reed warblers (*Acrocephalus arundinaceus*) nearly exclusively in the narrow reed-beds of small irrigation channels. We used a Telinga parabola dish with a Sennheiser ME 62 microphone and a Marantz PMD-620 MKII sound digital recorder (see Moskát et al., 2017

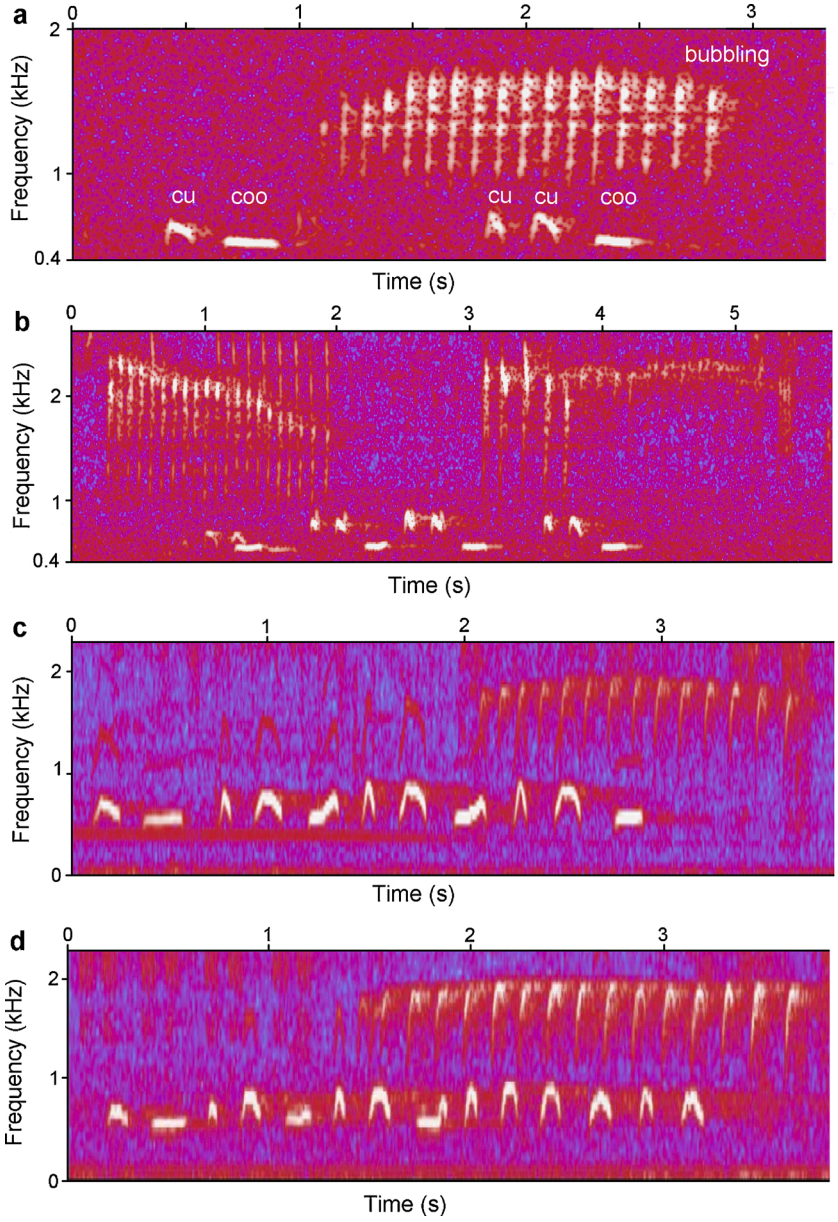

Fig. 1. Spectrograms of female common cuckoos' bubbling calls partly overlapping with males' 3-note ("cu-cu-coo") calls. (a) The bubbling call precedes the only 3-note call. (b) Two bubbling calls and four 3-note calls. (c) The 3-note calls precede the bubbling call. (d) A sequence of 3-note male cuckoo calls, starting with a normal 2-note ("cu-coo") call, and followed by a bubbling call of a female.

for more details) for recording cuckoo calls during the month of May each year between 2016 and 2020. We recorded these calls in a dense cuckoo population, with each recording site typically several kms from another. As both male (Moskát et al., 2017) and female (Moskát and Hauber, 2019) cuckoos are strictly territorial, therefore the chance for pseudoreplication (sensu Hurlbert, 1984) was almost nil.

For the analyses we used recordings with clearly audible female bubbling calls and male 3-note calls that were recorded in the mornings. The identification of duetting is not easy in species where males and females often use duetting song/call types alone. In such cases, for example, the SONG program (Masco et al., 2016) could be useful to reveal individuals' timing patterns. However, for our study, it was not difficult to detect duetting because we recorded almost all bubbling calls from focal females, together with the focal males' 3-note calls (see more details in Results). Typically, a female and male cuckoo were observed within a close distance (a few meters apart) from each other when these calls were uttered, as the subjects were sitting on a tree or flying together ("tandem flight", c.f. Mikulica et al., 2017). We used bubbling calls and the corresponding 3-note cuckoo calls from n = 13 duetting bouts (Fig. 1). Spectrograms of 24-bit .wav files were visualized in the Audacity 2.3.3 software. The visual separation of overlapping female and male calls was not difficult as their frequencies did not overlap (Fig. 1).

We then compared spectrogram parameters of 2-note and 3-note male cuckoo calls. Two-note male calls for these comparisons were also extracted from the same set of audio files that were used for the analysis of duetting. Following Fuisz and de Kort (2007) and Jung et al. (2014), we measured the minimum and maximum frequencies in notes, the duration of notes, as well as the pauses between notes. We selected sections of 2-note calls where at least three such type of calls were uttered continuously. We used the same principle for the 3-note calls, but when 2 such calls were uttered, we measured only one inter-call interval. Rarely only one 3-note call was uttered; in this case, of course, the inter-call interval could not be measured.

Variables were measured manually on spectrograms using the Audacity 2.3.3 software, and we calculated the mean value of 3 measurements per measurement type for each of the 2-note "cu-coo" calls per recording, and 1–3 calls from the 3-note "cu-cu-coo" call recording. We compared acoustic characteristics of note types with mixed linear models (the MIXED program in SPSS ver. 17), where minimum frequency (Hz), maximum frequency (Hz) and note length (s) were used as dependent variables in the models. Multivariate discriminant analysis was then used to compare this acoustical separation of the groups of note types again by their main characteristics: minimum frequency (Hz), maximum frequency (Hz), and length (duration) of the note (s) (DISCRIMINANT program in SPSS ver. 17).

We also compared both inter-element intervals (inter-note pauses) and pauses between successively emitted complete calls within 2- and 3-note calling bouts through two mixed linear models (MIXED prorgram in SPSS ver. 17). The dependent variables were: inter-note pause or inter-call pause and the fixed (predictor) factor was: pause length (s)). From the five call categories we used the "coo" element in the 3-note call for the reference category in the analyses.

We used SPSS ver. 17 for other statistical tests to characterize duetting: we used a binomial test (with equal probability assumption for categories) for the comparison of the initiator of the duetting (male/female as a binary response). We also applied the Mann-Whitney *U* test for comparisons of latencies per sex in duetting and binomial tests (random expectation: 50 %; two-tailed) for the comparison of frequencies of single and repeated bubbling calls with 3-note calls in duets.

Finally, we calculated spectrogram-based acoustic similarity of the different male notes from the 2- vs. 3-note calls using the Raven Pro 1.5 program (following Louder et al., 2019; Hauber et al., 2021; Moskát et al., 2021), and compared them by independent sample *t*-test (SPSS ver. 17.0).

3. Results

3.1. Vocal duetting in common cuckoos

In 67 % of the duetting recordings, the female call preceded male call (s), in 33 % the male call(s) preceded female call, but the difference was not significant [binomial test (two-tailed), predicted proportion: 50 %, P = 0.189, n = 21). In turn, in almost all cases, female and male calls of duetting typically overlapped (95 %, n = 20; in another case two bubbling calls rapidly followed each other, and both preceded the male call). The two call types followed each other rapidly (mean ± SD latency: 0.76 ± 0.53 s both when initiated by females; n = 14, and 1.30 ± 0.71 s and when initiated by males; n = 7; Mann-Whitney test: $U_{14,7} = 25.0$, P = 0.079). Frequently (90 %; n = 21), the male calls were repeated 2–3 times (rarely more), and the female calls were repeated less frequently (9%; n = 23; Fisher's exact test, two-tailed: P < 0.001). Elsewhere it has been reported that the 3-note call is extended into a long series of "cu-cu-cu-… -coo" call, consisting of 8–14 notes uttered rapidly (Lei et al., 2005), but we found only one case of such a long call in our recordings (Fig. 1d).

3.2. Acoustic comparisons of the elements of 2-note and 3-note common cuckoo calls

In 2-note cuckoo calls both notes were longer than the respective notes of the 3-note calls, and both minimum and maximum frequencies were higher in the 3-note calls than in the 2-note variants (Table 1; Table A.1 in Supplementary materials). The exception was the lowest frequencies between the last elements ("coo") in the 2-note and 3-note calls, which were not significantly different ($t_{147.78}$ = -0.780, p = 0.437; Table A.1 in Supplementary materials).

Multivariate discriminant analysis revealed two significant canonical discriminant functions (see details in Appendix B in Supplementary materials). One of them had a strong effect on the separation of the call types (function 1; corresponding eigenvalue: 9.066), while the second function has less importance (function 2; corresponding eigenvalue: 0.607). The plot of multivariate discriminant analysis revealed a similarity of the last, "coo" notes in both of the 2- and 3-note calls. However, the preceding "cu" notes showed greater variation (Fig. 2). The classification results showed the most correct classification for the first element in the 2-note cu-coo call ("cu"; 97 %). The "cu" elements in the

Table 1
Detailed characteristics of 2-note ("cu-coo") and 3-note ("cu-cu-coo") male common cuckoo calls as measured on spectrograms (mean ± SD).

	Minimum frequency (Hz)	Maximum frequency (Hz)	Duration length (s)	n
2-note call				
1st note ("cu")	538 ± 30.97	719 ± 38.37	0.114 ± 0.014	39
2nd note ("coo")	501 ± 26.73	576 ± 26.01	0.189 ± 0.017	39
3-note call				
1st note ("cu_1")	597 ± 80.11	866 ± 79.63	0.073 ± 0.015	28
2nd note ("cu_2")	589 ± 62.46	855 ± 57.02	0.119 ± 0.233	28
3rd note ("coo")	513 ± 28.04	616 ± 55.35	0.171 ± 0.025	28

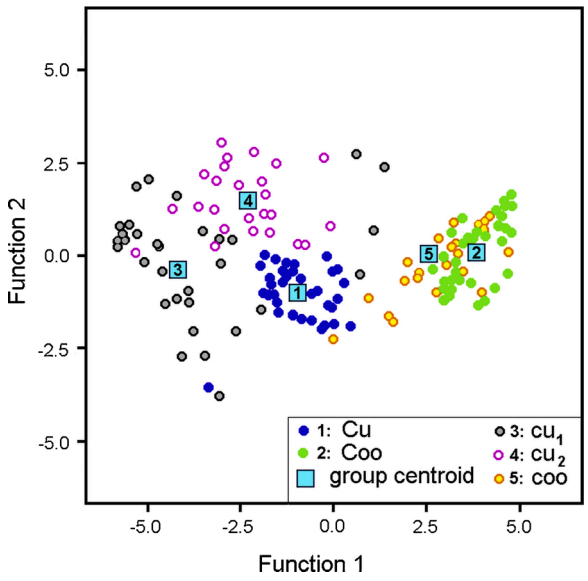

Fig. 2. A plot of discriminant scores of the elements of 2-note and 3-note male common cuckoo calls generated by canonical discriminant functions. (Elements of the calls: "Cu" and "Coo" in the 2-note variant, and "cu_1", "cu_2" and "coo" in the 3-note form).

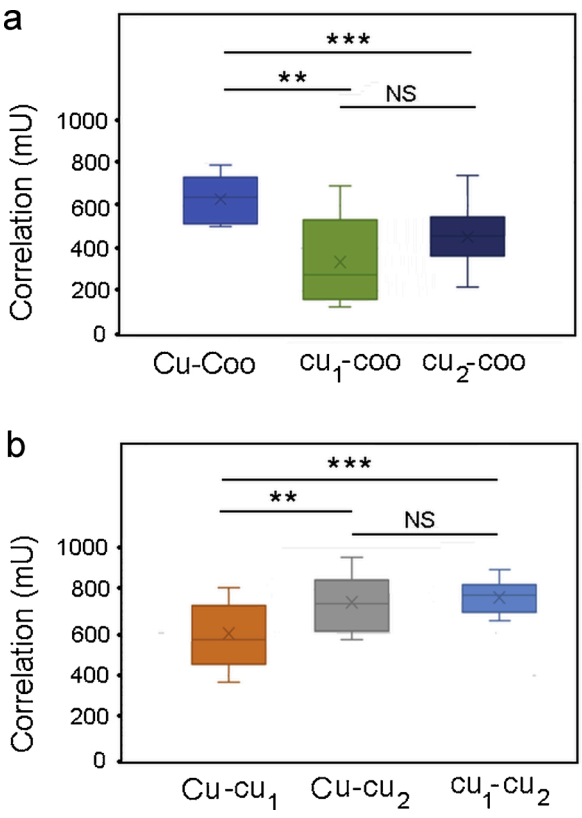

Fig. 3. Spectrogram correlation of call elements in 2-note ("Cu-Coo") and 3-note ("cu_1-cu_2-coo") male common cuckoo calls. (a) "cu" and "coo" notes. (b) Comparison of different "cu" notes. ("cu_1" and "cu_2" are the first and the second notes in the "cu-cu-coo" call, respectively).

3-note variant also separated well (75–86 %), and the lowest value was found for the "coo" element in the 3-note call, which was equally separated by 43 % in both of the two "coo" categories, i.e. in the 2-note and the 3-note calls (Table B.4 in Supplementary materials).

Apart from note lengths, inter-note intervals (pauses) were also significantly shorter in the 3-note version than in the 2-note variant (Table 2; within 2-note calls: $t_{65} = 5.93$, $p < 0.001$; second pause within the 3-note calls: 0.132 ± 0.034 SD, $t_{65} = 2.40$, $p = 0.019$). In the 3-note calls the inter-note intervals increased between the first and the second pauses ($t_{54} = -2.07$, $p = 0.044$). Inter-call intervals between complete calls were also longer in the 2-note than in the 3-note calls (Table 2; pauses between 2-note cu-coo calls: mean duration: 0.852 s ± 0.190 SD; between 3-note cu-cu-coo calls: 0.176 s ± 0.084 SD; $t_{39} = 13.01$, $p < 0.001$).

Finally, the spectrogram cross-correlations of the elements (notes) of the calls revealed that the "cu" and "coo" elements were more similar within the 2-note calls than in the 3-note calls (Fig. 3a; *t*-test: Cu-Coo vs. cu_1-coo: $t_{24} = 4.848$, $p < 0.001$; Cu-Coo vs. cu_2-coo: $t_{24} = 3.613$, $p = 0.001$; cu_1-coo vs. cu_2-coo: $t_{24} = -1.835$, $p = 0.079$). Spectrogram-similarity analysis also revealed that the 2-note call's "Cu" element was acoustically more similar to the second "cu_2", rather than the first "cu_1", in the 3-note call (Fig. 3b; mean correlations (mU) ± SD: cu-cu_1: 595.30 ± 146.25; cu-cu_2: 741.94 ± 122.36; - $t_{24} = 2.664$, $p = 0.014$).

4. Discussion

We showed that female and male common cuckoos use the female-specific bubbling call and a male-variant 3-note cuckoo call for duetting. The males' 3-note call ("cu-cu-coo") is less known in the literature (but see Xia et al., 2019). It appears to be the variant of their 2-note call, but the first two notes may also vary within one call. Males often repeat this extended call two-three times in the close vicinity of the female, while its minimum and maximum frequencies are increased and its duration is decreased in comparison to the similar elements in the 2-note cuckoo call. However, we also showed that the 3-note variant of the

Table 2
Intercall intervals (pauses) between call elements (notes) and between complete calls in two call types of common cuckoo males (2-note "cu-coo" and 3-note "cu-cu-coo"). Fixed effects are shown from two mixed linear models (dependent variables: internote pause and intercall pause; fixed factor: pause length (s).

Pause type (s)	"cu-coo" mean ± SD (n_i; n_p)	"cu-cu-coo" mean ± SD (n_i; n_p)	t	p
Internote	0.148 ± 0.020 (13; 39)	0.134 ± 0.031 (13; 56)	5.094	$p < 0.001$
Intercall	0.852 ± 0.190 (13; 26)	0.176 ± 0.084 (13; 15)	13.250	$p < 0.001$

n_i = number of cuckoo individuals; n_p = number of pauses.

2-note cuckoo call is not a simple repetition of the first element as it displays a somewhat elevated frequency in the "cu" note. Another important difference between the two male-call types is that the 2-note form is emitted with a slower speed when repeated sequentially relative to the 3-note variant. For this reason, humans also perceive it as a more rapid call than the 2-note variant, leading to its naming as also the "quick cu-cu-coo" call (Moskát and Hauber, 2019). Both frequency and speed modulations reflect some plasticity of common cuckoos' vocal signal production abilities.

In general, most intersexual duetting functions for joint territory defence or mate attraction (Hall, 2009). When there are more male than female birds present in a population, as seen in our common cuckoo population (Moskát and Hauber, 2019), duetting may serve as maintaining the pair-bond and/or as mutual mate defence (Seddon et al., 2002). In our population both males and females can initiate duetting, which suggests a function of pair-bond maintenance and/or mutual mate guarding. Accordingly, female bubbling calls preceded male calls in 67 % of cases, suggesting that females are also motivated in the maintenance of pair-bond. Although genetic studies revealed that most female common cuckoos were monogamous in a given study area and cuckoo density (e.g., Jones et al., 1997; Skjelseth et al., 2004), some were still polygynandrous, with both males or females having more than one mating partner (Marchetti et al., 1998). Specifically, in our study area we detected one-to-four tagged males around each female (Moskát and Hauber, 2019). Females' laying areas may also overlap in some extent, as revealed by both genetic (Kolecek et al., 2021) and GPS methods (Moskát et al., 2019). Finally, we frequently observed two males in the vicinity of a female in any time of the breeding season, showing competition amongst males for females (CM unpublished observations). Gärtner (1981) suggested a hierarchy amongst females (i.e., dominant, subdominant, and non-resident female cuckoos), and Riddiford (1986) simply distinguished territorial or non-territorial females. The resulting hierarchy may depend on female cuckoos' age, as young females appear to be more numerically constrained in their egg laying outputs than older females (Kolecek et al., 2021).

A previous study using a playback experiment with female bubbling calls, together with the presentation of a female cuckoo dummy, revealed that both sexes of wild cuckoos approached the dummy in most experimental trials (Moskát et al., 2020). In contrast, female cuckoos did not approach the speaker when 2-note male cuckoo calls in playback experiment was used, simulating male cuckoos as territory intruders (Moskát et al., 2017; Tryjanowski et al., 2018), but male cuckoos approached the speaker when it played the call of the female cuckoo as if for checking on the new female for potential mating (Lee et al., 2019; Moskát and Hauber, 2019). When female bubbling calls were played back without the presentation of dummy female cuckoo, males responded to bubbling calls with their 3-note call in 40 % of trials (Moskát and Hauber, 2019). However, in this experiment female and male cuckoos did not occur in a close vicinity (within a few meters) of each other when playbacks started, as we observed so between duetting partners in the natural cases (present study).

For these reasons it is plausible that duetting functions either to establish or strengthen the female-male mating bond in cuckoos. Although the appearance of new females attracts the attention of resident males (Lee et al., 2019), duetting keeps contact with an existing mate, at least temporarily (Baldassarre et al., 2016; Dowling and Webster, 2018; Sandoval et al., 2018), including in non-oscines (Penteriani, 2002). This may stabilize cuckoos' social relationships, as genetic analysis revealed less genetic promiscuity in cuckoos than expected, at least in females (Jones et al., 1997; Skjelseth et al., 2004; Feeney and Riehl, 2019).

The common cuckoo is, thus, also an example that a vocal non-learner avian species, with a limited set of call types, that can use duetting for social communication between female and male birds. Our results further revealed how this vocal non-learner species can increase its call repertoire by repeating a note to extend a call type, together with slight modulations of both frequency and speed. These syntactic changes in the basic, 2-note male-male advertisement ("cu-coo") call led to a semantic change, as the 3-note call ("cu-cu-coo") is specifically used for female-male communication.

Author statement

Both authors designed the study; CM recorded sound files, measured bioacoustic parameters and made statistical analyses with input from MEH; CM wrote the first draft of the manuscript with considerable participation from MEH; Both authors revised and approved the final version of the manuscript.

Funding details

The study was supported by the National Research, Development and Innovation Office, Hungary to CM (grant no. NN118194). Additional support was provided by the Hanse-Wissenschaftskolleg (Institute for Advanced Study), Germany to MEH, during the preparation of this manuscript.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Local ethical regulations and agreements were followed for fieldwork. All field work complied with the Hungarian laws, and the Middle-Danube-Valley Inspectorate for Environmental Protection, Nature Conservation and Water Management, Budapest, provided permission for research (permit no. PE/KTF/17190-3/2015).

Availability of data and materials

The datasets generated during and analysed for the current study are available from the corresponding author upon reasonable request.

Declaration of Competing Interest

The authors report no declarations of interest.

Appendix. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2021.104472.

References

Baldassarre, D.T., Greig, E.I., Webster, M.S., 2016. The couple that sings together stays together: duetting, aggression and extra-pair paternity in a promiscuous bird species. Biol. Lett. 12, 20151025 https://doi.org/10.1098/rsbl.2015.1025.

Benedetti, Y., Slezak, K., Møller, A.P., Morelli, F., Tryjanowski, P., 2018. Number of syllables in cuckoo *Cuculus canorus* calls: a test using a citizen science project. Sci. Rep. 8, 12872. https://doi.org/10.1038/s41598-018-31329-1.

Brenowitz, E.A., 1991. Evolution of the vocal control system in the avian brain. Semin. Neurosci. 3, 339–407. https://doi.org/10.1016/1044-5765(91)90030-R.

Brumm, H., Goymann, W., 2017. On the natural history of duetting in white-browed coucals: sex- and body-size-dependent differences in a collective vocal display. J. Ornithol. 158, 669–678. https://doi.org/10.1007/s10336-016-1429-0.

Dahlin, C.R., Benedict, L., 2014. Angry birds need not apply: a perspective on the flexible form and multifunctionality of avian vocal duets. Ethology 120, 1–10. https://doi.org/10.1111/eth.12182.

Delgado, M.M., Penteriani, V., 2007. Vocal behaviour and neighbour spatial arrangement during vocal displays in eagle owls (*Bubo bubo*). J. Zool. 271, 310. https://doi.org/10.1111/j.1469-7998.2006.00205.x.

Deng, Z., Lloyd, H., Xia, C., Møller, A.P., Liang, W., Zhang, Y., 2019. Components of variation in female common cuckoo calls. Behav. Process. 158, 106–112. https://doi.org/10.1016/j.beproc.2018.10.007.

Dowling, J., Webster, M.S., 2018. Acoustic and physical mate guarding have different effects on intruder behaviour in a duetting songbird. Anim. Behav. 135, 69–75. https://doi.org/10.1016/j.anbehav.2017.11.011.

Feeney, W.E., Riehl, C., 2019. Monogamy without parental care? Social and genetic mating systems of avian brood parasites. Phil. Trans. R. Soc. B374, 20180201 https://doi.org/10.1098/rstb.2018.020.
Fuisz, T.I., de Kort, S.R., 2007. Habitat-dependent call divergence in the common cuckoo: is it a potential signal for assortative mating? Proc. Roy. Soc. B 274, 2093–2097. https://doi.org/10.1098/rspb.2007.0487.
Gärtner, K., 1981. Das Wegnehmen von Wirstvogeleiern durch den Kuckuck *Cuculus canorus*. Ornithol. Mitt. 33, 115–131.
Hall, M.L., 2004. A review of hypotheses for the functions of avian duetting. Behav. Ecol. Sociobiol. 55, 415–430. https://doi.org/10.1007/s00265-003-0741-x.
Hall, M.L., 2009. A review of vocal duetting in birds. Adv. Stud. Behav. 40, 67–121. https://doi.org/10.1016/S0065-3454(09)40003-2.
Hauber, M.E., Taylor, D.M., Brawn, J.D., 2021. Variable or atypical? Comparing unusual songs of the tufted titmouse with a citizen-science database. J. Ornithol. 162, 313–316. https://doi.org/10.1007/s10336-020-01839-9.
Hurlbert, S.H., 1984. Pseudoreplication and design of ecological field experiments. Ecol. Monogr. 54, 187–211. https://doi.org/10.2307/1942661.
Jarvis, E.D., 2013. Evolution of brain pathways for vocal learning in birds and humans. In: Bolhuis, J.J., Everaert, M. (Eds.), Birdsong, Speech, and Language. Exploring the Evolution of Mind and Brain. MIT Press, Cambridge, Massachusetts, pp. 63–107.
Jedlikowski, J., Polak, M., Brambilla, M., Rek, P., 2021. Vocal and non-vocal behavior interact differently in territorial strategies of two sympatric Rallidae species. J. Ornithol. 162, 243–254. https://doi.org/10.1007/s1033 6-020-01808-2.
Jones, D.A., Gibbs, H.L., Matsuda, T., Brooke, M., de, L., Uchida, H., Bayliss, M.J., 1997. The use of DNA fingerprinting to determine the possible mating system of an obligate brood parasitic bird, the cuckoo (*Cuculus canorus*). Ibis 139, 560–562. https://doi.org/10.1111/j.1474-919X.1997.tb04672.x.
Jung, W.J., Lee, J.W., Yoo, J.C., 2014. "Cu-coo": can you recognize my stepparents? A study of host-specific male call divergence in the common cuckoo. PLoS One 9, e90468. https://doi.org/10.1371/journal.pone.0090468.
Kolecek, J., Pialkovová, R., Piálek, L., Sulc, M., Hughes, A.E., Brlik, V., Pocházka, P., Pougayová, M., Capek, M., Sosnovcová, K., Stétková, G., Valterová, R., Honza, M., 2021. Spatiotemporal patterns of egg laying in the common cuckoo. Anim. Behav. 177, 107–116. https://doi.org/10.1016/j.anbehav.2021.04.021.
Langmore, N.E., 1998. Functions of duet and solo songs of female birds. Trend. Ecol. Evol. 13, 134–140. https://doi.org/10.1016/S0169-5347(02)02611-3.
Lee, J.W., Kim, H.N., Yoo, S., Yoo, J.C., 2019. Common cuckoo females may escape male sexual harassment by color polymorphism. Sci. Rep. 9, 7515. https://doi.org/10.1038/s41598-019-44024-44026.
Lei, F.-M., Zhao, H.-F., Wang, A.-Z., Yin, Z.-H., Payne, R.B., 2005. Vocalizations of the common cuckoo *Cuculus canorus* in China. Acta. Zool. Sin. 51, 31–37.
Logue, D.M., Krupp, D.B., 2016. Duetting as a collective behavior. Front. Ecol. Evol. 4, 7. https://doi.org/10.3389/fevo.2016.00007.
Louder, M.I.M., Balakrishnan, C.N., Louder, A.N.A., Driver, R.J., London, S.E., Hauber, M.E., 2019. An acoustic password enhances auditory learning in juvenile brood parasitic cowbirds. Curr. Biol. 29, 4045–4051. https://doi.org/10.1016/j.cub.2019.09.04.
Marchetti, K., Nakamura, H., Gibbs, H.L., 1998. Host-race formation in the common cuckoo. Science 282, 471–472. https://doi.org/10.1126/science.282.5388.471.
Marton, A., Fülöp, A., Bán, M., Hauber, M.E., Moskát, C., 2021. Female common cuckoo calls dampen the mobbing intensity of great reed warbler hosts. Ethology 127, 286–293. https://doi.org/10.1111/eth.13126.
Masco, C., Allesina, S., Mennill, D.J., Pruett-Jones, S., 2016. The Song Overlap Null Model Generator (SONG): a new tool for distinguishing between random and non-random song overlap. Bioacoustics 25, 29–40. https://doi.org/10.1080/09524622.2015.1079734.
Maurer, G., Smith, C., Süsser, M., Magrath, R.D., 2008. Solo and duet calling in the pheasant coucal: sex and individual call differences in a nesting cuckoo with reversed size dimorphism. Aust. J. Zool. 56, 143–149. https://doi.org/10.1071/ZO08049.
Mikulica, O., Grim, T., Schulze-Hagen, K., Stokke, B.G., 2017. The Cuckoo: The Uninvited Guest. Wild Nature Press, Plymouth.
Møller, A.P., Morelli, F., Mousseau, T.A., Tryjanowski, P., 2016. The number of syllables in Chernobyl cuckoo calls reliably indicate habitat, soil and radiation levels. Ecol. Indic. 66, 592–597. https://doi.org/10.1016/j.ecolind.2016.02.037.
Moskát, C., Hauber, M.E., 2019. Sex-specific responses to simulated territorial intrusions in the common cuckoo: a dual function of female acoustic signaling. Behav. Ecol. Sociobiol. 73, 60. https://doi.org/10.1007/s00265-019-2665-0.
Moskát, C., Elek, Z., Bán, M., Geltsch, N., Hauber, M.E., 2017. Can common cuckoos discriminate between neighbours and strangers by their calls? Anim. Behav. 126, 253–260. https://doi.org/10.1016/janbehav.2017.02.013.
Moskát, C., Bán, M., Fülöp, A., Bereczki, J., Hauber, M.E., 2019. Bimodal habitat use in brood parasitic common cuckoos (*Cuculus canorus*) revealed by GPS telemetry. Auk 136, 1–12. https://doi.org/10.1093/auk/uky019.
Moskát, C., Hauber, M.E., Růžičková, J., Marton, A., Bán, M., Elek, Z., 2020. Female-female aggression and male responses to the two colour morphs of female common cuckoos. Sci. Nat. 107, 28. https://doi.org/10.1007/s00114-020-01680-3.
Moskát, C., Taylor, D.M., Hauber, M.E., 2021. Effective conspecific communication with aberrant calls in the common cuckoo (*Cuculus canorus*). Behav. Ecol. Sociobiol. 75, 7. https://doi.org/10.1007/s00265-020-02946-6.
Odom, K., Mennill, D.J., 2010. Vocal duets in a nonpasserine: an examination of territory defence and neighbour–stranger discrimination in a neighbourhood of barred owls. Behaviour 147, 619–639. https://doi.org/10.1163/000579510X12632972452424.
Payne, R.B., 1971. Duetting and chorus singing in African birds. Ostrich: J. African. Ornithol. 42 (S1), 125–146. https://doi.org/10.1080/00306525.1971.9633401.
Penteriani, V., 2002. Variation in the function of eagle owl vocal behaviour: territorial defence and intra-pair communication? Ethol. Ecol. Evol. 14, 275–281. https://doi.org/10.1080/08927014.2002.9522746.
Riddiford, N., 1986. Why do cuckoos *Cuculus canorus* use so many species of hosts? Bird Study 33, 1–5. https://doi.org/10.1080/00063658609476883.
Rogers, A.C., Langmore, N.E., Mulder, R.A., 2007. Function of pair duets in the eastern whipbird: cooperative defense or sexual conflict? Behav. Ecol. 18, 182–188. https://doi.org/10.1093/beheco/arl070.
Sandoval, L., Juárez, R., Villarreal, M., 2018. Different messages are transmitted by individual duet contributions and complete duets in a species with highly overlapped duets. Open Ornithol. J. 11, 56–67. https://doi.org/10.2174/1874453201811010056.
Seddon, N., Butchart, S.H.M., Odling-Smee, L., 2002. Duetting in the subdesert mesite *Monias benschi*: evidence for acoustic mate defence? Behav. Ecol. Sociobiol. 52, 7–16. https://doi.org/10.1007/s00265-002-0488-9.
Sikora, J.G., Moyer, M.J., Omland, K.E., Rose, E.M., 2021. Large female song repertoires and within-pair song type sharing in a temperate breeding songbird. Ethology 12, 166–175. https://doi.org/10.1111/eth.13115.
Skjelseth, S., Moksnes, A., Røskaft, E., Gibbs, H.L., Taborsky, M., Taborsky, B., Honza, M., Kleven, O., 2004. Parentage and host preference in the common cuckoo *Cuculus canorus*. J. Avian Biol. 35, 21–24. https://doi.org/10.1111/j.0908-8857.2004.03219.x.
Thorpe, W.J., 1967. Vocal Imitation and Antiphonal Song and Its Implications. Proc. Internat. Ornithol. Congr., Oxford, pp. 245–263.
Tryjanowski, P., Morelli, F., Osiejuk, T.S., Møller, A.P., 2018. Functional significance of cuckoo *Cuculus canorus* calls: responses of conspecifics, hosts and non-hosts. PeerJ 6, e5302. https://doi.org/10.7717/peerj.5302.
van den Heuvel, I.M., Cherry, M.I., Klump, G.M., 2013. Individual identity, song repertoire and duet function in the crimson-breasted shrike (*Laniarius atrococcineus*). Bioacoustics 22, 1–15. https://doi.org/10.1080/09524622.2012.701041.
Wheeldon, A., Szymański, P., Budka, M., Osiejuk, T.S., 2020. Structure and functions of yellow-breasted boubou (*Laniarius atroflavus*) solos and duets. PeerJ 8, e10214. https://doi.org/10.7717/peerj.10214.
Wheeldon, A., Szymański, P., Osiejuk, T.S., 2021. Yellow-breasted boubous (*Laniarius atroflavus*) jointly defend territories with male-led duets against stranger pairs, males and females. Ethology 127, 176–186. https://doi.org/10.1111/eth.13116.
Xia, C., Deng, Z., Lloyd, H., Møller, A.P., Zhao, X., Zhang, Y., 2019. The function of three main call types in common cuckoo. Ethology 125, 652–659. https://doi.org/10.1111/eth.12918.
York, J.E., Davies, N.B., 2017. Female cuckoo calls misdirect host defences towards the wrong enemy. Nat. Ecol. Evol. 1, 1520–1525. https://doi.org/10.1038/s41559-017-0279-32.