



Are both notes of the common cuckoo's call necessary for familiarity recognition?

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ARTICLE INFO

Keywords:

Neighbour-stranger discrimination
Dear-enemy effect
Individual recognition
Playback
Sound analysis
Acoustic manipulation

ABSTRACT

Common cuckoos (*Cuculus canorus*) are best known for their simple two-note calls (“cu-coo”), which are uttered only by males during the breeding season. A previous playback study revealed that territorial males were more tolerant toward playbacks of the calls of familiar, neighbouring individuals than toward unfamiliar, stranger simulated intruders, exhibiting the classical “dear-enemy” phenomenon. Here we experimentally assessed whether the acoustic cues for familiarity recognition are encoded in the first and/or second note of these simple calls. To do so, we played mixed sound files to radio-tagged cuckoos, where the first part of the two-note calls was taken from strangers and the second part from neighbours, or vice versa. As controls, we used behavioural data from two-note neighbour and two-note stranger call playbacks. Cuckoos responded consistently to the two types of mixed sound files. When either the first or second note of the call was taken from a stranger and the other note from a neighbour, they responded to these sound files similarly to two-note playbacks of strangers: they approached the speaker of the playbacks more closely and the calling response-latency to playbacks was longer than to familiar controls. These findings point to the importance of both notes in familiarity recognition. We conclude that familiarity recognition in male common cuckoos needs the complete structure of the two-note cuckoo call, which is characteristic for this species.

1. Introduction

Categorical and individual recognition plays an important role in the social behaviour of animals and can be found in a wide range of taxa (Tibbetts and Dale, 2007). Conspecifics may recognize each other through several sensory modalities, such as visually (Kondo and Izawa, 2014; Kohda et al., 2015; Charpentier et al., 2017), by olfactory cues (Bonadonna et al., 2007; Carazo et al., 2008; Golüke et al., 2016), or acoustically (Bee 2012; Sharpe et al., 2013). For acoustic social recognition, birds are the best-studied examples to date (Catchpole and Slater, 2008).

Birds have evolved complex acoustic signalling and auditory perceptual systems (Stevens, 2013). For example, syllables are often learned and shared between neighbouring individuals, such as in palm cockatoos (*Probosciger aterrimus*; Zdenek et al., 2015). In songbirds, many species join different syllables to form complex phrases/songs, which allow them to differentiate their song from that of their

neighbours. For example, song sparrows (*Melospiza melodia*) can use song types for individual recognition and learn many such songs, even artificially composed sequences, seemingly not limited by the capacity of their memory (Stoddard et al., 1992). In the skylark (*Alauda arvensis*) neighbouring males show specific group signatures in their song, and territorial males show less aggression toward those individuals with shared song types (Briefer et al., 2010). This suggests that shared syllables may facilitate familiarity with the song producer, leading to different behavioural outcomes. Furthermore, zebra finches (*Taeniopygia guttata*) prefer familiar songs over new songs of conspecifics (reviewed in Hauber et al., 2010); carrion crows (*Corvus corone*) respond more intensively to unfamiliar than familiar conspecific calls (Wascher et al., 2012), and are able to discriminate between reliable and non-reliable conspecifics, depending on the circumstances (Wascher et al., 2015). In the crimson-breasted shrike (*Laniarius atrococcineus*) male-female duetting of pairs helps individual recognition of neighbours and intruders (Heuvel et al., 2013). Finally, in playbacks to a songbird with

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a small song repertoire, the ortolan bunting (*Emberiza hortulana*), territorial birds identified their neighbours as unfamiliar intruders when the frequency of their songs was slightly modified experimentally (Osiejuk, 2014).

Even in non-songbirds (except Psittaciformes and Trochiliformes), which often use genetically fixed calls and cannot learn a new sound type (Brenowitz, 1991), categorical and/or individual recognition has also been repeatedly demonstrated; such examples include king penguins (*Aptenodytes patagonicus*; Aubin and Jouventin, 1998), little owls (*Athene noctua*; Hardouin et al., 2006), and corncrakes (*Crex crex*; Budka and Osiejuk, 2013). However, not all species use frequency modulation to identify conspecifics. Although the corncrake is able to discriminate between calls of neighbours and strangers (Budka and Osiejuk, 2013), this species does not use an individually specific frequency parameter within call syllables for individual recognition (Budka and Osiejuk, 2014).

Brood parasites belonging to Cuculiformes are also suspected to be vocal non-learners (Brenowitz, 1991; Jarvis et al., 2000). Avian brood parasitism is a special case of interspecific bird–bird interactions, where one species, the brood parasite, utilizes the parental ability of the other species, the host, to incubate, feed, and fledge its descendants (Davies, 2000). This relationship is dynamic both in real time and in an evolutionary context, where both sides evolve adaptations to the other, termed as a co-evolutionary arms race (Stoddard and Hauber, 2017).

The obligate brood parasitic common cuckoo (*Cuculus canorus*) is historically and culturally famous for its male's simple two-note calls ("cu-coo"), repeated over and over (Lei et al., 2005). Although the brood parasitic lifestyle of the common cuckoo has been known since at least antiquity, as Aristotle mentioned (Schulze-Hagen et al., 2009) and the "cu-coo" call is one of the most popular bird sound in human culture (Møller et al., 2016), its functions are still partly unknown. It may play a role in male–female communications (Chance, 1940), in attracting females (Wyllie, 1981) and it was described as a general advertising call (Lei et al., 2005). It may also serve as a tool for species recognition in areas where several similar cuckoo species live in sympatry (Lack, 1968). Recently we showed that the cuckoo's general call ("cu-coo") plays an important role in male–male interactions, as common cuckoos conformed to neighbour–stranger discrimination: cuckoos were more responsive and, in particular, more aggressive toward the playback calls of unfamiliar intruders than toward those of their familiar neighbours (Moskát et al., 2017). Consequently, the common cuckoo could be a model species to study how social status and individuality are conveyed by simple calls. In the present study we investigated if cuckoo call composition, which is variable at the level of the individual (Jung et al., 2014; Li et al., 2017; Zsebök et al., 2017), encodes information that may enable to recognize familiar individuals. We hypothesize that (i) familiarity information is encoded in the first part of the cuckoo call ("cu") or that (ii) familiarity information is encoded in the second part of the two-note call ("coo"). Alternatively, (iii) familiarity information is encoded in both parts of the cuckoo call.

2. Methods

2.1. Study area and season

The study was conducted around Apaj (47° 6′ 53.9″ N; 19° 5′ 21.2″ E), ca. 30–50 km south of Budapest, in central Hungary, where common cuckoos parasitize great reed warblers (*Acrocephalus arundinaceus*) at high frequencies (over 50% parasitism rate; Moskát and Honza, 2000; Zölei et al., 2015). The hosts breed locally in narrow, 2–5 m wide reed belts along both banks of small irrigation channels, and cuckoos can be observed in tree rows and patches of woodland vegetation along the channels. Cuckoos form partially overlapping territories along this linear, channel-side habitat (Moskát et al., 2017). Fieldwork was conducted during the 2017 breeding season from May 8 to May 23, but we also used published experimental control data from a similar period in

the previous year (Moskát et al., 2017). These controls (control neighbour) for ten cuckoos showed how focal birds responded to the playback of radio-tagged neighbours, carried out with the same methods (see below). Our study period overlapped the most intensive time interval of cuckoo parasitism, i.e. the highest availability of host nests in the egg-laying stage (Moskát et al., 2006).

2.2. Radio telemetry

To identify neighbours we used radio telemetry, as we had tagged either or both the focal bird and its neighbour. We caught 33 cuckoos in 2017 using mist nests and conspecific-call playbacks, in the early morning or just before sunset, and equipped 18 male cuckoos with VHF radio telemetry using Pip3 transmitters (type 392) by Biotrack Ltd. (Wareham, Dorset, U.K.). We also used data of 10 tagged cuckoos from the previous year. A tag weighting ca. 1.2 g (about 1% of the male common cuckoo's weight), including a 18 cm-long wire antenna, was fixed via tail mounting with factory-provided strings and glue (Loctite 4860), so the tags would be lost at the next moulting cycle together with the central tail feathers. The sex of radio-tracked adult cuckoos was identified by plumage characteristics (Svensson et al., 2010) when they were captured. In the field male cuckoos were identified by their "cu-coo" call, as it is exclusively uttered by male cuckoos. We located and identified the tagged neighbouring cuckoos with a Sika receiver, extended with flexible 3-element Yagi and omnidirectional magmount (car) antennas (Biotrack Ltd). Our previous work on radio tagged cuckoos suggested that the extent of cuckoo territories varied between 1 km and 2 km (rarely longer) along the channels (Moskát et al., 2017). For this reason, we considered a cuckoo less than 0.5 km away from the focal bird as a neighbour, and further than 10 km as a stranger, regardless of their exact spatial location. The location of the loudspeaker in playback experiments might affect neighbour recognition in strictly territorial birds (Lovell and Lein, 2005; Hardouin et al., 2006). However, cuckoos show high mobility within their overlapping home ranges including several host territories, and therefore the occurrence of neighbouring cuckoos is plausible within a 1–2 km range along the channels (Moskát et al., 2017).

2.3. Call recordings

We recorded male common cuckoo calls with a Telinga Universal parabola dish with Rycote Hi Wind Cover, equipped with a Sennheiser ME-62 microphone and K6 powering module. We recorded the sounds with a Marantz PMD-620 MKII sound recorder with a 48 kHz sampling rate and 24-bit quality. We also externally attached a FEL MX mono preamp module to amplify the acoustic signals. We uploaded sample call sequences of common cuckoos recorded in 2017 to the Xeno-Canto public sound library (www.xeno-canto.org; codes: XC380809, XC380974, XC380993, and XC381024).

2.4. Playback experiments

There is a lack of consistency among different studies on the terminology of the acoustic units of a cuckoo call. The unit of such a call ("cu-coo") is termed differently, e.g. meaning two syllables (Fuisz and de Kort, 2007; Jung et al., 2014), one compound syllable (Møller et al., 2016), or two notes (Payne, 1986; Lei et al., 2005; Wei et al., 2015). Xia et al. (2016) described syllables of other *Cuculus* species as a composition of notes. Sometimes the terms note and syllable were used interchangeably (Verboom, 2009). In the present study we describe a "cu-coo" call as one syllable, containing two elements, i.e. the "cu" and "coo" notes (Fig. 1). We played 2-min cuckoo calls in wav 16-bit format to focal cuckoo individuals, using a Lenovo tablet and a JBL Xtreme loudspeaker (40 W), connected with a 20-m audio cable. The loudspeaker was set up on a tree ca. 1.5 m in height. Peak sound volume was standardized 90 dB (A) SPL, measured at 1 m by a Voltcraft SL-100

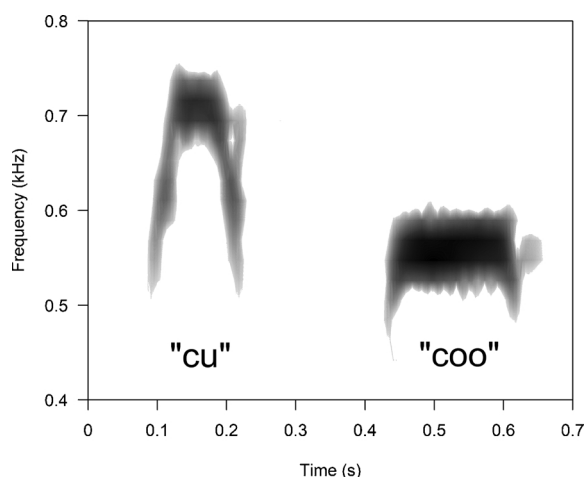


Fig. 1. Spectrogram of a male common cuckoo's two-note call ("cu-coo").

sound level meter.

During playback experiments one observer, naïve to sound type, observed the focal bird, while another observer handled the telemetry receiver and continuously monitored the focal bird. The observers stayed hidden behind bushes about 20 m from the loudspeaker. At the beginning of the experiment the focal bird was about 40–50 m from the observers. We measured three variables during the playbacks which proved to be useful in the separation of strangers and neighbours in our previous study on cuckoos (Moskát et al., 2017): the closest distance to the loudspeaker when the focal bird approached it ("closest distance", m), the time interval between the start of the playback and the first movement of the focal bird ("movement latency", s) and when the focal bird started calling ("sound latency", s).

We played 2-min playback files to cuckoos (Fig. 2a), following the method used by Moskát et al. (2017). (The basic elements of a sound

file contained 3×10 s different phrase sections (ca. 6–8 syllables in a phrase, three different sequences followed each other, altogether 30 s of playing time) from the same cuckoo individual. This set was repeated twice in a playback with a 15 s break between each set. Altogether, a sound file had 2 min of playing time.) The sound files were edited with the program Audacity version 2.1 (<http://audacity.sourceforge.net>). In mixed experimental sound files, we created a set of combinations for either the stranger or neighbour of focal birds (or vice versa) based on their recorded "cu-coo" calls; consequently, we could use sound files for playback where the stranger bird gave the "cu" note and the neighbour bird gave the "coo" note for the experimental file ("mixed-1"), or vice versa ("mixed-2"; Fig. 2b). In both types of these experimental files we used the structure of the first file containing the "cu"s, and inserted the second note from the second individual accordingly. In these sound files no manipulations were applied, but noise was filtered out below 300 Hz, and the amplitude was standardised with respect to peak amplitude (c.f. Moskát et al., 2017). For all sound files we selected sequences of syllables with the male "cu-coo" calls only, avoiding other types of cuckoo calls (e.g. "gowk" calls, c.f. Lei et al., 2005).

In the field we played each type of experimental files (mixed-1 and mixed-2) only once, and only to one focal bird to avoid pseudoreplication (Kroodsma, 1989). Each focal bird was tested with both experimental files (mixed-1 played first and then mixed-2, or mixed-2 played first and then mixed-1), having a 2-minute rest between the two playbacks. In these paired experiments the notes were used from the same cuckoo individuals, but the two types of notes were used oppositely (see above; Fig. 2b). This way mixed-1 files were played first to 6 focal birds and to 8 focal birds second. The sequence of playing the two sound files was random.

To compare host responses to playbacks we used the unmanipulated stranger or neighbour cuckoo calls as controls. We played either stranger or neighbour sound files (controls; see above) only once for a cuckoo, and no other experiments were done with these cuckoo individuals to avoid potential pseudoreplication (c.f. Kroodsma, 1989).

2.5. Statistical analyses

As we played both of the experimental files randomly to focal birds, we applied binary logistic regression when tested the potential effects of playing order on cuckoo responses to mixed-1 and mixed-2 playbacks. In this analysis the categorical (dichotomous) variable was playing order, and the predictor variables were "movement latency", "closest distance" and "sound latency".

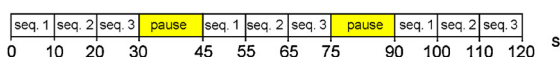
We compared cuckoos' responses to playbacks ("movement latency", "closest distance" and "sound latency") by categories (mixed-1, mixed-2, neighbours and strangers). We carried out a MANOVA using General Linear Models (GLM). We tested for the effects of group membership on each of the different dependent variables by ANOVAs. Fisher's Least Significant Difference post hoc tests were applied to test for differences among group means. All statistical tests were carried out with the SPSS Statistics Base 17.0 program package (SPSS Inc., Chicago, IL).

3. Results

Altogether we tested 38 male cuckoos as focal birds in our playbacks, namely 14 strangers, 10 neighbours, and 14 experimental birds. Each bird was tested once, except for experimental birds in 2017, to which both the mixed-1 and mixed-2 sound files were played in a random order. In the 14 experiments mixed-2 sound files were played first to 8 cuckoos and to 6 focal birds the second time. Binary logistic regression revealed that none of the predictor variables ("movement latency", "closest distance", and "sound latency") were affected significantly by playing order (Table 1), so we combined our data from different playing orders for further analyses.

We tested the four treatment groups of cuckoos together (strangers,

(a) The structure of a playback file



(b) The composition of an experimental playback file

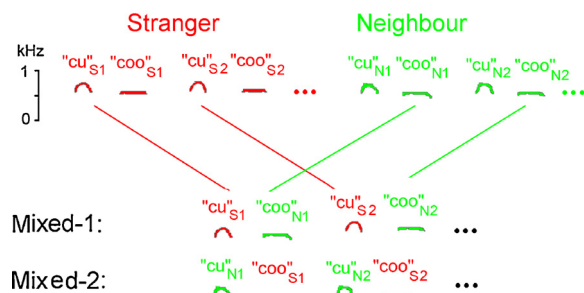


Fig. 2. Composition of playback files used for the study. (a) The general structure of a playback file used either for playing stranger or neighbour calling sequences for the focal bird; the same basic structure was also used for mixed experimental files. Three different call sequences (seq. 1, seq. 2 and seq. 3) from the same individual cuckoo, each with length of 10 s, are played continuously, and then repeated two times after 15 s breaks. The total length of a playback file is 2 min. (b) Construction of a mixed sound file from a stranger and a neighbour's calling sequences. The figures illustrate the simplified spectrograms of a stranger, neighbour and mixed experimental files type 1 (mixed-1), when the first notes are taken from a stranger and the second notes from a neighbour. The mixed experimental file type 2, denoted as mixed-2, was constructed similarly, but the first notes were taken from a neighbour, and the second notes from a stranger's call sequence.

Table 1

Parameter estimates of binary logistic regression on cuckoo responses to two types of experimental playback files, mixed-1 (a) and mixed-2 (b), where the independent variable was playing order (the first or the second).

(a)						
Mixed-1	B	S.E.	Wald	df	P	Exp(B)
latency	−0.019	0.074	0.064	1	0.801	0.981
closest distance	−0.233	0.128	3.329	1	0.068	0.792
sound latency	−0.004	0.028	0.016	1	0.899	0.996
intercept	3.899	2.369	2.708	1	0.100	49.329

(b)						
Mixed-2	B	S.E.	Wald	df	P	Exp(B)
latency	0.020	0.043	0.208	1	0.648	1.020
closest distance	0.072	0.083	0.758	1	0.384	1.075
sound latency	−0.024	0.054	0.199	1	0.655	0.976
intercept	−1.026	1.692	0.367	1	0.544	0.359

neighbours, mixed-1, and mixed-2 experiments). Of the response variables, none proved to be a significant predictor of subject responses to playback treatments in the MANOVA (Table 2a), but “sound latency” was almost significant in the univariate tests of between-subject effects (ANOVAs; Table 2b). However, post hoc comparisons indicated that the variable “closest distance” was significantly different between strangers and neighbours, but was not significantly different among strangers and between both experimental groups (see Table 2c; Fig. 3a). Focal birds responded by their “cu-coo” calls to our playbacks. The variable “sound latency” was significantly shorter for neighbours than to the other treatment groups (Table 2c; Fig. 3b). These findings suggest that cuckoos respond similarly to the playback of experimental files and to stranger calls.

4. Discussion

We experimentally compared the relative importance of the first and second parts of the simple call of male common cuckoos (“cu” and “coo”) in recognizing familiar neighbours and unfamiliar intruders, as our previous study demonstrated the classical “dear-enemy” behaviour in this species (Moskát et al., 2017). These new experiments and analyses confirmed that, while cuckoos show high interest in unfamiliar cuckoo calls (“checking out the stranger”), they appear to know their neighbours and “greet” them by quick “cu-coo” calls, demonstrating familiarity recognition of the neighbouring intruder. Here we focused on how cuckoos might recognize familiarity status acoustically through their simple two-note calls. We discovered that both parts of their calls appear to be necessary for the recognition of familiarity status (neighbour or stranger).

Theoretically, compound acoustic syllables may function in one unit, or by pieces. An example is the song of blackcaps (*Sylvia atricapilla*), which consists of two parts, differing in intensity, frequency and temporal parameters (Linossier et al., 2015). Although there were expectations in that study that the two parts of the blackcap songs encoded different information, these parts functioned similarly when they were played alone. As the two-note call is characteristic for the common cuckoo, we exchanged the familiarity status of the signallers in an experimental sound file in the first or second half of the “cu-coo” call, consequently in all syllables in a calling sequence (Fig. 1). This structure of the experimental playback calls preserved the species-specific two-note call structure. Similarly, the three-note call of the Eurasian collared dove (*Streptopelia decaocto*) resembles the common cuckoo call, even in the bandwidth of its frequencies, but collared dove playbacks had no effect on cuckoo behaviour (Moskát et al., 2017).

Zsebök et al. (2017) found that characteristics of seven sound parameters suggested for comparison of the common cuckoo’s two-note

Table 2

MANOVA results concerning the three variables describing the responses of common cuckoos to playbacks, including four treatments, differing in the type of playback types: strangers (control), neighbours (control), mixed-1 and mixed-2 experimental. ((a) Multivariate tests, (b) tests of between-subject effects, and (c) post hoc tests with Fisher’s least significant difference for variables.) The three variables (“movement latency”, “closest distance” approach to loudspeaker, and “sound latency”) were transformed before the analyses by logarithmic and square root transformations to fit the normal distribution (see Results for more details).

(a) Multivariate tests						
	Value	F	Hypothesis df	Error df	P	Observed power
Pillai’s trace	0.298	1.765	9	144.000	0.080	0.779
Wilk’s lambda	0.714	1.846	9	112.103	0.068	0.677
Hotelling’s trace	0.382	1.898	9	134.000	0.057	0.812
Roy’s largest root	0.330	5.287	3	48.000	0.003**	0.909

(b) Tests of between-subject effects						
Dependent variable	Type III Sum of Squares	df	Mean Square	F	P	Observed power
Movement latency (s)	1.012	3	0.337	0.815	0.492	0.213
Closest distance (m)	9.496	3	3.165	1.763	0.169	0.429
Sound latency (s)	3.984	3	1.328	2.665	0.058	0.614

(c) Post hoc tests						
Dependent variable	Factor (I)	Factor (J)	Mean difference (I-J)	S.E.	P	
movement latency ¹	strangers	neighbours	−0.146	0.266	0.587	
		mixed-1	−0.338	0.243	0.171	
		mixed-2	−0.306	0.243	0.215	
	neighbours	mixed-1	−0.192	0.266	0.474	
		mixed-2	−0.160	0.266	0.551	
	mixed-1	mixed-2	0.033	0.243	0.894	
closest distance ²	strangers	neighbours	−1.192	0.556	0.037*	
		mixed-1	−0.209	0.508	0.682	
		mixed-2	−0.174	0.508	0.733	
	neighbours	mixed-1	0.983	0.556	0.084	
		mixed-2	1.018	0.556	0.074	
	mixed-1	mixed-2	−0.351	0.508	0.945	
sound latency ¹	strangers	neighbours	0.734	0.292	0.015*	
		mixed-1	0.147	0.267	0.585	
		mixed-2	0.001	0.267	0.996	
	neighbours	mixed-1	−0.587	0.292	0.050*	
		mixed-2	−0.733	0.292	0.016*	
	mixed-1	mixed-2	0.146	0.267	0.588	

* = Significant at $P < 0.05$.

** = Significant at $P < 0.01$.

¹ = Logarithmic transformation (natural logarithm) was applied.

² = Square root transformed.

advertising calls showed high variation among individuals, consequently they seem to be suitable for encoding individual differences. Other studies on common cuckoos also showed strong individual differences in their calls (Jung et al., 2014; Li et al., 2017). Common cuckoo calls may also differ by population and habitat (frequency and duration parameters, Fuisz and de Kort, 2007; lowest frequency and bandwidth of the second note, Wei et al., 2015). Additional experimental and behavioural studies are nonetheless needed to reveal exactly how the individual signatures are encoded, how they express individual identity, and how territorial males perceive and respond to

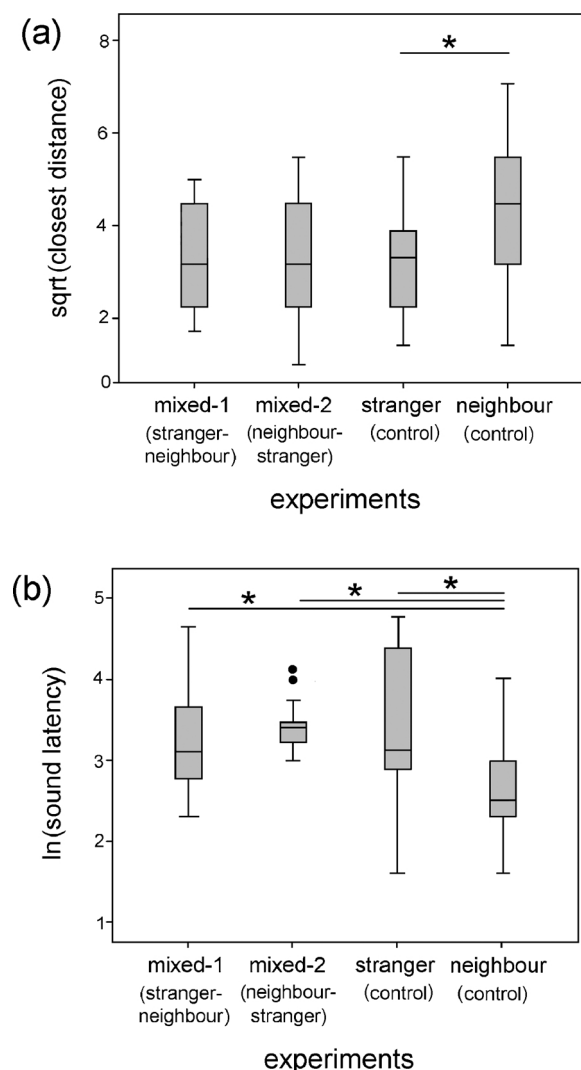


Fig. 3. Box-plots of cuckoo response variables “closest distance” approach (a) and “sound latency” (b) to playbacks (strangers, neighbours, mixed-1 and mixed-2 experimental sound files; see Methods for more details). Asterisks indicate significant differences with Fisher's least significant difference post hoc test at the $P < 0.05$ level. The box-plot shows the median (central horizontal line), 75th and 25th percentile (top and bottom of the box) and the maximum and minimum values (top and bottom whisker), respectively. Outliers, observations 1.5 * interquartile range (IQR) outside the central box, are shown by dots.

different individuals of the same familiarity or unfamiliarity status (i.e. true individual recognition).

Acknowledgments

The authors thank István Zsoldos for assistance with the fieldwork, Danielle Allen for assistance with editing, Christina Zdenek and Miks Abolins-Abols for their comments on the manuscript, and Kirill Márk Orci for his helpful advice. The study was supported by the National Research, Development and Innovation Office, Hungary to CM (grant No. NN118194). Additional funding was provided by the US National Science Foundation to MEH (grant No. IOS 1456524). All 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).

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