

RESEARCH ARTICLE



WILEY

Female common cuckoo calls dampen the mobbing intensity of great reed warbler hosts

Attila Marton^{1,2} | Attila Fülöp^{2,3} | Miklós Bán^{1,3} | Márk E. Hauber⁴ | Csaba Moskát⁵

¹Department of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen, Hungary

²Juhász-Nagy Pál Doctoral School, University of Debrecen, Debrecen, Hungary

³MTA-DE Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen, Hungary

⁴Department of Evolution, Ecology, and Behavior, School of Integrative Biology, University of Illinois at Urbana-Champaign, Urbana, IL, USA

⁵MTA-ELTE-MTM Ecology Research Group, A Joint Research Group of the Hungarian Academy of Sciences, The Biological Institute of the Eötvös Loránd University and the Hungarian Natural History Museum, Budapest, Hungary

Correspondence

Attila Marton, Department of Evolutionary Zoology and Human Biology, University of Debrecen, Egyetem tér 1, H-4032 Debrecen, Hungary.
Email: martonatilla2010@gmail.com

Funding information

Nemzeti Kutatási Fejlesztési és Innovációs Hivatal, Grant/Award Number: OTKA NN118194; National Science Foundation, Grant/Award Number: IOS #1953226; Új Nemzeti Kiválóság Program, Grant/Award Number: ÚNKP-19-3-I-DE-368

Editor: Wolfgang Goymann

Abstract

To avoid mobbing attacks by their hosts during egg laying, some avian brood parasites have evolved traits to visually and/or acoustically resemble predator(s) of their hosts. Prior work established that reed warblers (*Acrocephalus scirpaceus*), a small host species of the brood parasitic common cuckoo (*Cuculus canorus*), delayed returning to the nest when confronted by either the calls of the female cuckoo or that of the predatory sparrowhawk (*Accipiter nisus*). It remains less clear, however, whether female cuckoo calls also suppress the nest defences of larger and more aggressive hosts. Such hosts typically attack vigorously, and can even hurt the brood parasitic intruders, instead of fleeing in the face of danger. Here, we tested whether the female cuckoo calls dampen mobbing intensity in a much larger *Acrocephalus* host of the common cuckoo, the great reed warbler (*A. arundinaceus*). We presented great reed warbler pairs with female common cuckoo models at their nests without and then with playing back the female-specific bubbling calls of the cuckoo. As controls, we tested the hosts' responses to harmless collared dove (*Streptopelia decaocto*) models, also without and then with the playbacks of dove calls. We found that the playback of female brood parasite calls reduced the aggression of hosts towards the cuckoo models as compared to model presentations without female calls, but we detected no such effect of the control calls with dove models. Our results revealed that female cuckoo calls effectively suppress the antiparasitic responses of great reed warbler hosts, which could aid parasites to approach the nest undiscovered and to evade the costly attacks of this large host. Therefore, the female call can be regarded as a general part of the cuckoo's trickery repertoire for successful parasitism.

KEYWORDS

acoustic mimicry, brood parasitism, front-line defence, host aggression, nest defence

1 | INTRODUCTION

Enemy recognition plays a pivotal role in shaping the coevolutionary relationship between brood parasites and their hosts, eliciting either fighting or fleeing behavioural responses from the hosts. This behavioural dichotomy gains a focal function in the breeding

season (Ellis-Fellege et al., 2013; Pavel, 2006; Zhang et al., 2020), when the benefits of protecting the current brood (i.e., fighting) are put in balance against the benefits of potential future broods (i.e., fleeing). This trade-off implies that any investment by parents in their current offspring decreases their ability to invest in future offspring (Trivers, 1974). Therefore, parental recognition and

engagement of a potential brood parasite require a decision by the parent.

Decision errors (e.g., failing to recognise a parasite, or conversely, identifying an avian predator as a nest parasite) might be especially costly for the hosts of the brood parasitic Cuculidae cuckoos, since many of these brood parasitic species evolved vocal and plumage traits to resemble their hosts' avian predators in an effort to successfully parasitise host nests (Gluckman & Mundy, 2013). In theory, if a host identifies a threat as a brood parasite, the best response is to fight and drive the brood parasite away from the nest, therefore increasing current fitness without threatening parental survival (i.e., front-loaded antiparasitic defences; Feeney & Langmore, 2013). In contrast, if the parent identifies the threat as a predator, the best action is to flee in order to secure parental survival and, hence, future fitness. Misidentifying a brood parasite as a predator and fleeing might bring about negative fitness consequences through a higher chance of being parasitised, while misidentifying a predator as a brood parasite and attacking it might lead to an early demise of the adult host due to predation.

When the nest is approached by a heterospecific enemy, parents rely on a wide array of cues to assess the predatory vs. parasitic threat posed by the intruder. Some of the cues and contexts influencing the decision to flee or to stay and protect the brood include the stage of the brood (Campobello & Sealy, 2010; Moskát, 2005; Lawson et al., 2020), the identity of the enemy (e.g., reptile, bird or mammal; Kleindorfer et al., 2005; Strnad et al., 2012), its distance from the focal individual or its nest (Kryštofková et al., 2011), the type of threat (e.g., predator of adult birds, nest predator or brood parasite; Campobello & Sealy, 2018; Kleindorfer et al., 2005; Trnka & Prokop, 2010; Lawson et al., 2020), prior information regarding the occurrence of the threat (both on an individual and social level; Fontain & Martin, 2006; Davies & Welbergen, 2009; Campobello et al., 2017) and/or the reproductive senescence of parents (Clutton-Brock, 1984; Graham & Shutler, 2019).

The common cuckoo (*Cuculus canorus*, "cuckoo" from hereafter) is a well-known obligate brood parasite that lays its eggs in the nests of other bird species, coercing these hosts to incubate parasitic eggs, and feed and rear the lone cuckoo nestling at the cost of their own brood's failure (Wyllie, 1981). Hosts evade brood parasitism by evolving traits to prevent parasitism (e.g., secretive nesting, mobbing adult parasites; Feeney et al., 2012; Moksnes & Røskaft, 1988; Welbergen & Davies, 2011) or to lessen costs once their nests have been parasitised (e.g., the recognition and ejection of brood parasitic eggs; Bártol et al., 2002). Intense aggression towards the brood parasite (reviewed in Campobello et al., 2017) might ensure host reproductive success even in species where no egg or chick rejection has evolved (Medina & Langmore, 2015). In turn, cuckoos have evolved several adaptations to overcome host defences, such as rapid egg deposition and laying in the afternoons (instead of mornings, like their hosts do), egg mimicry and resemblance to avian predators, giving rise to a coevolutionary arms race between brood parasites and their hosts (Davies, 2015). Whether visual resemblance to predators has adaptive value is still debated (Davies & Welbergen, 2008; Li

et al., 2015; Ma et al., 2018; Trnka & Prokop, 2012; Trnka et al., 2012, 2015; Welbergen & Davies, 2011).

While the adaptive similarity in appearance between the adult cuckoo and the sparrowhawk (*Accipiter nisus*) was one of the foci of the past two decades of research on brood parasites and their hosts (Davies, 2015; Trnka et al., 2012; Welbergen & Davies, 2011), the acoustic components of this similarity were only recently examined. These studies have now revealed that sounds emitted by brood parasites play an important role in conspecific communication (Moskát et al., 2017, 2020; Moskát & Hauber, 2019; Yu et al., 2019), and also as a means to increase the breeding success of the brood parasite. For example, a recent study demonstrated that cuckoos likely eavesdrop on the alarm calls of their hosts to locate host nests (Marton et al., 2019), while another study revealed that female cuckoos manipulate the behaviour of their hosts through their calls which are similar to those of the sparrowhawk (York & Davies, 2017). This latter study provided experimental evidence that a small host species, the reed warbler (*Acrocephalus scirpaceus*, ca. 12 g), increased its vigilance, returned to their nest later and was more likely to accept foreign eggs when threatened by the calls of female cuckoos, a sound similar to that of their aerial predator, the sparrowhawk, than when presented with the calls of the collared dove (*Streptopelia decaocto*; "dove" from hereafter) used as a sympatric, harmless control. Moreover, the female cuckoo calls had the same effect as sparrowhawk calls had on the attentiveness of wintering great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) outside the breeding season, two species that are only seldom parasitised by the cuckoo (Grim et al., 2014). Tits constitutes an important part of the sparrowhawk's diet during winter (Krams et al., 2020; Newton, 1986), when the cuckoos are on their sub-Saharan wintering grounds (Bán et al., 2018).

The reed warbler avoided possible predatory threats (e.g., sparrowhawk) through increased vigilance (i.e., peeking out of the nest) and an increased latency to return to the nest once flushed (York & Davies, 2017). However, the great reed warbler (*Acrocephalus arundinaceus*, ca. 32 g), a relatively larger host of the common cuckoo (ca. 100 g), is typically more aggressive towards both predators and brood parasites than the smaller warbler species, and attacks cuckoos near its nest more often (Moksnes et al., 1991; Røskaft et al., 2002; Trnka & Prokop, 2010, 2012), sometimes with fatal consequences for the brood parasites (Molnár, 1944; Šulc et al., 2020). Therefore, the coping strategy of a larger and more aggressive host might differ markedly and predictably from the behavioural response of a smaller, more threat-avoidant host.

To test whether or not the bubbling call of the female cuckoo has a greater effect on the aggressive mobbing behaviours of the larger great reed warblers than it had on a smaller host (e.g., reed warblers), we performed experimental cuckoo intrusion trials at great reed warbler nests. Specifically, we measured the aggressiveness (i.e., mobbing intensity) of great reed warblers towards cuckoo and dove decoys, before and during the playback of female cuckoo bubbling calls, and the calls of the dove used as control, respectively. Based on prior work on several host species (Li et al., 2015; Ma et al., 2018;

Trnka & Prokop, 2012), we predicted greater response intensity against the 3D-printed model of the cuckoo relative to the control decoy. In turn, given that the bubbling call of the female cuckoo mimics the sparrowhawk's calls (York & Davies, 2017), we predicted reduced response intensity by the hosts to the cuckoo model presentations coupled with the female call's playback vs. without the playback, and a generally low level of mobbing intensity towards the dove decoy, irrespective of the presence or absence of playbacks of dove calls.

2 | MATERIAL AND METHODS

2.1 | Study area

We carried out our study in central Hungary, around Apaj village (47°6'53.9"N; 19°5'21.2"E), ca. 40 km south of Budapest. In this region, great reed warblers face high rates of parasitism by cuckoos since decades (ca. 50%; Zölei et al., 2015). Here, hosts nest in narrow reed beds running along both sides of small irrigation channels, lined with tall trees serving as vantage points for eavesdropping cuckoos (Moskát & Honza, 2000; Marton et al., 2019).

2.2 | Experimental set-up

To test whether the female cuckoo's bubbling call (Moskát & Hauber, 2019) has a negative effect on host mobbing intensity, we presented 3D-printed common cuckoo or dove models as a control to great reed warblers at their nests (following Marton et al., 2019). We performed experimental trials at great reed warbler nests ($n = 61$), during the laying and early incubation stages. Great reed warblers and, other closely related *Acrocephalus* species maintain a high level of aggression towards adult cuckoos during their breeding cycle (Moskát, 2005; Li et al., 2015; Ma et al., 2018; but see Trnka & Prokop, 2012), likely because cuckoos may predate active nests to force hosts to restart breeding and to secure suitable laying opportunities for themselves (Schulze-Hagen, 1992; Soler et al., 2017). We had to exclude 19 trials (~30%) from the final data set; these were conducted at nests where great reed warblers altogether failed to turn up after 20 min, as these nests were subsequently deemed as deserted. We collected information regarding the number of great reed warbler and cuckoo eggs per clutch, clutch initiation date, and date and time of the experiments, with all experiments being performed in May 2019, between 7:00 and 12:00 or 17:00 and 20:00 hrs local time.

Cuckoo males are always grey, whereas females are polymorphic, being either grey or rufous, or of some intermediary form between (Moskát et al., 2020). The rufous female morph is common at our study area (up to 60%) and is mobbed by great reed warblers with an intensity similar to the grey morph (Honza et al., 2006). We used 3D-model cuckoo decoys painted with acrylics to resemble rufous cuckoo females, similarly to Lee et al. (2019). These decoys

were produced by printing life-size common cuckoo models (3D Quick Printing, UK) and collared dove models downloaded from Thingiverse.com (modified to fit the support pole of the cuckoo models), using an Ultimaker 2+ 3D printer and plain white Ultimaker PLA filament (see Marton et al., 2019 for more details). Researchers extensively use model birds in experiments with brood parasites and hosts (see a review in Campobello et al., 2017). Although the surface texture of the decoy may affect the intensity of host reactions (e.g., Němec et al., 2015), several studies have established that taxidermic mounts of cuckoos, decoys made of polystyrene or real live cuckoos were similarly attacked by different songbird species in field experiments (Honza et al., 2006; Tryjanowski et al., 2018).

We placed a randomly selected cuckoo or dove decoy next to a great reed warbler nest (cuckoo trials: $n = 22$; dove trials: $n = 20$), at a distance of ca. 20 cm, and a Nikon Coolpix AW130 Digital Camera Recorder, at 3–5 m from the nest. We recorded the mobbing behaviours of great reed warblers for 2 min upon discovering the cuckoo or dove decoy, after which we played back the female cuckoo's bubbling calls for the cuckoo decoy, or the call of the dove for the dove decoy for 2 min, on a JBL Xtreme 40 W Loudspeaker. The average time lag ($\pm$ SD) between the two 2-min periods was 31 ± 33 s. We used 2-min-long acoustic files for playback, each containing ca. 2-s-long bubbling calls (three calls within 30 s), and this section was repeated two times with 15-s inter-section silent periods. A similar structure was also used for the 2-min dove control files (see more details of the playback in Moskát & Hauber, 2019; Moskát et al., 2020). To reduce pseudoreplication, we used three different rufous cuckoo and three dove decoys, and six different bubbling call and six dove call recordings chosen randomly. All calls were recorded by us locally between 2014 and 2018. We subsequently analysed the videos by counting the numbers of adult great reed warblers present during the trial and the numbers of different mobbing behaviours separately: "churr" alarm calls, bill snaps, pecks and physical contact attacks against the decoys per the 2-min trials.

2.3 | Statistical analyses

To test the effect of the female cuckoo bubbling call on the mobbing intensity of the hosts, we first calculated the total mobbing intensity of the hosts towards the 3D decoys both before and during the 2-min-long period when great reed warblers were exposed to playback calls. We expressed total mobbing intensity by summing the number of "churr" calls, bill snaps, pecks and attacks during 2 min. We built a general linear mixed-effects model with a zero-inflated Poisson error distribution, with total mobbing intensity as a dependent variable, and three two-level fixed factors as explanatory variables: the number of great reed warblers mobbing the 3D decoy (one member or both members of the pair), treatment (cuckoo or dove) and playback call (before or during playback). Additionally, we tested all the two-way interactions with the fixed factor treatment. Nest ID and irrigation channel (site) ID ($n = 4$) were entered as random factors in the model to control both for repeated measurements at

the same nests during trial periods and for potential spatial autocorrelation in the parasitism rate among irrigation channels. The initial model that contained all the above-listed variables (i.e., full model) was then simplified by sequentially removing variables with non-significant effects ($p > .05$) until reaching the minimal adequate model that included only significant interactions, significant main effects or non-significant main effects involved in significant interactions.

We performed all statistical analyses using the R statistical environment (ver. 4.0.2, R Core Team, 2020). Mixed-effects modelling was carried out using the R package "glmmTMB" (Brooks et al., 2017). Predictor significance levels were calculated using the Wald tests with an ANOVA (type II) as implemented in the "car" R package (Fox & Weisberg, 2019). Model fit assumptions for both full and minimal models were assessed using diagnostic plots and functions included in the "DHARMa" R package (Hartig, 2020). *Post-hoc* tests for significant interactions were carried out using the R package "emmeans" (Lenth, 2020).

3 | RESULTS

Mobbing intensity showed extensive variation between treatments and playback periods, and great reed warblers used different forms of mobbing with varying intensities in response to the different treatments (Table 1).

We found a significant interaction between treatment and playback period (Table 2). *Post-hoc* comparison of contrasts between

mobbing levels for the different periods (i.e., before and during playback) of the two treatment types (i.e., cuckoo vs. dove) revealed that there was no significant difference in total mobbing intensity before and during the dove call playback ($\beta = 0.336$, $SE = 0.420$, $t = 0.799$, $p = .427$), whereas great reed warblers mobbed significantly less during the cuckoo bubbling call playback than before it was broadcast ($\beta = -0.607$, $SE = 0.052$, $t = -11.692$, $p < .001$; Figure 1). Although total mobbing intensity seemed to be greater when both members of the great reed warbler pair were present, compared to when only one of the hosts was mobbing the decoys, after removing the non-significant interaction between treatment $\times$ number of great reed warblers present from the full model, the main effect of the number of great reed warblers present also became non-significant in the minimal model (Table 2).

4 | DISCUSSION

Our results revealed that the female cuckoo bubbling call decreased the levels of aggression displayed by great reed warbler hosts towards cuckoos at their nests. This is in line with the results of a study performed on a smaller and less aggressive host species, the reed warbler. This smaller host, when experimentally exposed to the bubbling calls of female cuckoos or to the calls of the sparrowhawk, reduced its nest attendance and avoided a potential predator by returning later to the nest, as well as accepted foreign eggs more often compared to when the calls of the collared dove or common cuckoo

TABLE 1 Mean, median, standard deviation (SD) and range of mobbing variables produced by great reed warblers at their nests, before and during the playback of the female common cuckoo bubbling call at a rufous morph cuckoo decoy and of the calls of the collared dove at a collared dove decoy, as counted from video recordings.

Treatment	Variable	Before playback				During playback				V	p	p _{adj}
		Mean	Median	SD	Range	Mean	Median	SD	Range			
Cuckoo	No. of "churr" calls	0.41	0.00	1.71	0–8	0.00	0.00	0.00	0–0	3	.500	.580
	No. of bill snaps	29.09	19.00	31.04	0–123	14.46	2.00	26.73	0–120	169.5	<.001	<.001
	No. of pecks	7.32	0.00	15.99	0–70	5.41	0.00	15.74	0–72	45.5	.290	.580
	No. of attacks	14.05	6.50	19.98	0–80	6.41	0.00	16.25	0–67	120	<.001	<.001
	<i>Total mobbing intensity</i>	50.86	43.00	50.54	0–203	26.27	7.00	43.96	0–191			
Dove	No. of "churr" calls	0.75	0.00	1.45	0–5	1.10	0.00	4.08	0–18	11	.938	1.000
	No. of bill snaps	0.45	0.00	1.40	0–5	0.10	0.00	0.45	0–2	3	.500	1.000
	No. of pecks	0.10	0.00	0.45	0–2	0.00	0.00	0.00	0–0	1	1.000	1.000
	No. of attacks	0.55	0.00	1.82	0–8	0.00	0.00	0.00	0–0	6	.250	1.000
	<i>Total mobbing intensity</i>	1.85	0.00	3.18	0–12	1.20	0.00	4.07	0–18			

Note: Comparisons of mobbing behaviours were carried out using paired Wilcoxon signed rank tests, and significance levels (p) were corrected for multiple comparisons using Holm correction (p_{adj}). Significant differences ($p \leq .05$) are marked with bold, while variable names and values marked with italics are composite variables and values showing the total mobbing intensity of great reed warblers expressed through the sum of the different mobbing responses recorded.

TABLE 2 Results of the full and minimal adequate models showing that great reed warblers (GRW) exhibited a higher mobbing intensity towards the cuckoo decoys than towards the dove decoys and that mobbing intensity towards the cuckoo decoys decreased if the cuckoo female bubbling call was played back

Predictors	Full model						Minimal adequate model					
	β	SE	z value	χ^2	df	p	β	SE	z value	χ^2	df	p
Conditional model												
Intercept	1.543	0.845	1.826				3.363	0.352	9.562			
GRW present (both members)	2.023	0.920	2.199	4.089	1	.043						
Treatment (dove)	-2.255	1.006	-2.243	17.764	1	<.001	-3.867	0.616	-6.277	35.276	1	<.001
Playback (with playback)	-0.608	0.052	-11.706	133.143	1	<.001	-0.607	0.052	-11.692	132.392	1	<.001
Treatment (dove):GRW present (both members)	-1.412	1.305	-1.082	1.170	1	.279						
Treatment (dove):playback (with playback)	0.911	0.434	2.101	4.413	1	.036	0.943	0.423	2.228	4.963	1	.026
Zero-inflated model												
Intercept	-1.257	0.405	-3.105				-1.107	0.355	-3.120			
Random effects												
Residual variance	1.78						1.85					
Nest ID	2.3						2.36					
Channel ID	0						0					
N (Nest ID)	42						42					
N (Channel ID)	4						4					
Observations	84						84					

Significant effects ($p \leq .05$) are marked with bold.

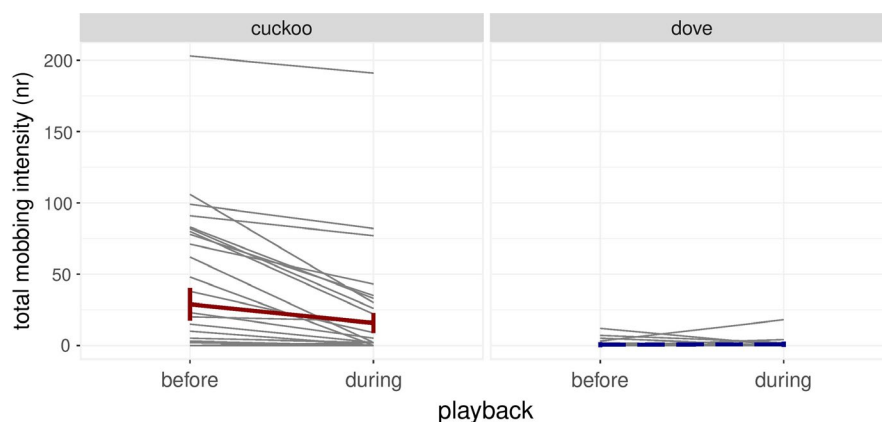


FIGURE 1 Change in the total mobbing intensity (i.e., sum of all mobbing responses) of great reed warblers against adult rufous common cuckoo and collared dove decoys, for the two periods of 2 min before and during the playback of female cuckoo bubbling calls or dove calls, respectively. Grey lines indicate the changes at the hosts' responses at individual nests before and during species-specific playback calls, whereas the red continuous and the dashed blue lines indicate changes in average mobbing intensity against the cuckoo or dove decoys (model predicted means $\pm$ SE) [Colour figure can be viewed at wileyonlinelibrary.com]

male calls (non-bubbling) were played back to them as a control (York & Davies, 2017). Although in the aforementioned study the mobbing intensity of reed warblers towards the cuckoo decoy, measured as mobbing call rate, did not differ before and during playbacks, in our study the focal species is more aggressive and 2–3 times heavier than the reed warbler (Cramp, 1992; Leisler & Schulze-Hagen, 2011).

Also, apart from producing a very loud mobbing call, great reed warblers readily pecked and attacked the cuckoo decoy before the onset of the bubbling playbacks, whereas its total mobbing intensity still dropped by more than half when the bubbling calls were initiated.

Although our results show a consistent drop in total mobbing intensity against the cuckoo decoy during the period when the bubbling

call was broadcast compared to the period without the bubbling call, we acknowledge that our study design has some shortcomings also. Specifically, our experimental set-up lacked a fully factorial design due to the unusually low number of active great reed warbler nests in our study area in 2019, and was not symmetrical (i.e., silent periods always preceded playbacks). This latter issue, however, might have a negligible effect on our results, because although the bubbling call playback decreased the mobbing intensity of great reed warblers against the cuckoo decoy, we found no such effect during the trials with dove decoys and the dove playbacks, albeit they were presented in same order as in the case of the cuckoo treatment. Also, it is reasonable to assume that a symmetrical design (i.e., having a treatment group with playback preceding the silent period) would have resulted in a biased sampling, since it is likely that the less aggressive great reed warblers would not have approached the cuckoo decoy coupled with bubbling calls. As a possible improvement for future studies with similar design and facing a parallel design conundrum, we recommend inserting a second silent (non-playback) period after the playback periods.

The great reed warbler is a socially monogamous species, in which high-quality males mate with multiple females (Sejberg et al., 2000). Monogamous great reed warbler males invest more in nest defence than polygamous males do, while females defend their nests more vigorously than males, and do so regardless of their mating status (Trnka & Prokop, 2010). The mating status of great reed warblers in our study was unknown, but we recorded the number of adults mobbing the decoys. Since this number of mobbing great reed warblers at the nest was not a statistical predictor of total mobbing intensity, we assume that most of the mobbing was performed by females. Additionally, the treatment (i.e., cuckoo vs. dove) was assigned randomly to each nest; therefore, it is likely that the social mating status of the hosts did not confound our findings.

It is worth noting that, despite the few known cases when the great reed warblers managed to kill a cuckoo by drowning it in water (Molnár, 1944; Šulc et al., 2020), the mobbing of live female cuckoos by great reed warblers seemingly has little effect on the success rate of parasitic attempts, as cuckoos still manage to lay eggs in the host nests, even when both parents of this larger host are attacking them fiercely (Jelínek et al., 2020).

These results suggest that the acoustic mimicry of predatory sparrowhawk calls by female cuckoos has an adaptive function, which is additional to the raptorial plumage mimicry of the grey morph of adult cuckoos from both sexes (Trnka & Grim, 2013; Trnka et al., 2012, 2015). Critically, the acoustic mimicry functions for both the grey (York & Davies, 2017) and rufous (this study) morph of adult female cuckoos. Grey cuckoos appear similar to sparrowhawks (e.g., Trnka & Prokop, 2012; Trnka et al., 2012), and this mimicry may already defend cuckoos from host aggression to some extent (Welbergen & Davies, 2011), although plumage mimicry is less effective against the more aggressive and larger *Acrocephalus* species (Li et al., 2015; Ma et al., 2018; Trnka & Prokop, 2012). Rufous female cuckoos, in turn, despite having barred underparts and yellow eyes, do not resemble sparrowhawks or small falcons in colouration (Trnka & Grim, 2013; Trnka et al., 2015). Therefore, the lack of

sparrowhawk-plumage mimicry could create an uneven playing field against rufous females relative to females of the grey morph, might hinder successful parasitism and might explain why this morph is usually rarer than the grey morph. Future studies should aim to address these differences, by experimentally testing the reactions of various host species towards the two female cuckoo colour morphs (e.g., Thorogood & Davies, 2012), presented to the hosts alongside the bubbling call or the control calls of a harmless species.

The female cuckoo's bubbling call seems to be a multifunctional signal, being important in interspecific cuckoo–host relationships, as well as in conspecific communication (Deng et al., 2019; Moskát & Hauber, 2019). The bubbling call might play a role in the context of mate attraction (Moskát & Hauber, 2019; Xia et al., 2019) and could also function as a territorial signal for other conspecific females (Davies, 2015; Moskát et al., 2020). A previous study (York & Davies, 2017) tested an interspecific function of female cuckoo calls against a small host, the reed warbler, while our results revealed that this call also effectively dampened the mobbing responses of a large host, the great reed warbler. Our results point to the adaptive value of acoustic mimicry of female cuckoo calls even against more aggressive hosts, especially against those host species where the raptorial plumage mimicry of the grey cuckoo morph is less effective (Li et al., 2015; Ma et al., 2018; Trnka & Prokop, 2012).

ETHICS STATEMENT

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 work complied with Hungarian law and the Middle-Danube-Valley Inspectorate for Environmental Protection, Nature Conservation and Water Management, Budapest, provided permission for research (permit no. PE/KTFO/3097-10/2020).

ACKNOWLEDGEMENTS

We are grateful to Csongor I. Vágási for his valuable comments on an earlier version of the manuscript and Danielle Allen for polishing the English of the manuscript. We thank the editor and two anonymous reviewers for their comments and suggestions on earlier versions of the manuscript. The study was funded by the National Research, Development and Innovation Office, Hungary, through a grant awarded to CM (grant no. OTKA NN118194), and by the New National Excellence Programme Scholarship awarded to AM (grant no. ÚNKP-19-3-I-DE-368). Additional support was provided by the US National Science Foundation (IOS #1953226 to MEH).

CONFLICT OF INTEREST

We declare no competing interests.

AUTHOR CONTRIBUTIONS

AM, CM and MEH devised the study, AM and MB collected the data, AF performed the statistical analyses, and AM wrote the first draft and revised manuscript with considerable input and the approval of the final version by all authors.

DATA AVAILABILITY STATEMENT

The data analysed in this study is available online at Figshare.com [https://doi.org/10.6084/m9.figshare.13489209].

ORCID

Attila Marton  <https://orcid.org/0000-0002-8768-2248>

Attila Fülöp  <https://orcid.org/0000-0001-5337-336X>

Miklós Bán  <https://orcid.org/0000-0002-6275-7928>

Márk E. Hauber  <https://orcid.org/0000-0003-2014-4928>

Csaba Moskát  <https://orcid.org/0000-0002-8800-4975>

REFERENCES

- Bán, M., Moskát, C., Fülöp, A., & Hauber, M. E. (2018). Return migration of common cuckoos (*Cuculus canorus*) between breeding grounds in Hungary and wintering grounds in Africa as documented by non-PTT GPS technology. *Journal of Ornithology*, 159, 337–344. <https://doi.org/10.1007/s10336-017-1508-x>
- Bártol, I., Karcza, Z., Moskát, C., Røskft, E., & Kisbenedek, T. (2002). Responses of great reed warblers *Acrocephalus arundinaceus* to experimental brood parasitism: The effects of a cuckoo *Cuculus canorus* dummy and egg mimicry. *Journal of Avian Biology*, 33, 420–425. <https://doi.org/10.1034/j.1600-048X.2002.02945.x>
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modelling. *The R Journal*, 9, 378–400. <https://doi.org/10.3929/ethz-b-000240890>
- Campobello, D., & Sealy, S. G. (2010). Enemy recognition of reed warblers (*Acrocephalus scirpaceus*): Threats and reproductive value act independently in nest defence modulation. *Ethology*, 116, 498–508. <https://doi.org/10.1111/j.1439-0310.2010.01764.x>
- Campobello, D., & Sealy, S. G. (2018). Evolutionary significance of antiparasite, antipredator and learning phenotypes of avian nest defence. *Scientific Reports*, 8, 10569. <https://doi.org/10.1038/s41598-018-28275-3>
- Campobello, D., Sealy, S. G., & Welbergen, J. A. (2017). Anti-brood parasite defences: The role of individual and social learning. In Soler, M. (Ed.), *Avian brood parasitism: Behaviour, ecology, evolution and coevolution* (pp. 421–436). Springer International Publishing. https://doi.org/10.1007/978-3-319-73138-4_23
- Clutton-Brock, T. H. (1984). Reproductive effort and terminal investment in iteroparous animals. *American Naturalist*, 123, 212–229. <https://doi.org/10.1086/284198>
- Cramp, S. (Ed.) (1992). *Handbook of the birds of Europe, the Middle East and North Africa*, Vol. 6. Oxford University Press.
- Davies, N. B. (2015). *Cuckoo. Cheating by nature*. Bloomsbury Publishing.
- Davies, N. B., & Welbergen, J. A. (2008). Cuckoo-hawk mimicry? An experimental test. *Proceedings of the Royal Society B: Biological Sciences*, 275, 1817–1822. <https://doi.org/10.1098/rspb.2008.0331>
- Davies, N. B., & Welbergen, J. A. (2009). Social transmission of a host defense against cuckoo parasitism. *Science*, 324, 1318–1320. <https://doi.org/10.1126/science.1172227>
- Deng, Z., Lloyd, H., Xia, C., Møller, A. P., Liang, W., & Zhang, Y. (2019). Components of variation in female common cuckoo calls. *Behavioural Processes*, 158, 106–112. <https://doi.org/10.1016/j.beproc.2018.10.007>
- Ellis-Fellege, S. N., Burnam, J. S., Palmer, W. E., Clay Sisson, D., & Carroll, J. P. (2013). Fight or flight: Parental decisions about predators at nests of northern bobwhites (*Colinus virginianus*). *The Auk*, 130, 637–644. <https://doi.org/10.1525/auk.2013.12227>
- Feeney, W. E., & Langmore, N. E. (2013). Social learning of a brood parasite by its host. *Biology Letters*, 9, 20130443. <https://doi.org/10.1098/rsbl.2013.0443>
- Feeney, W. E., Welbergen, J. A., & Langmore, N. E. (2012). The frontline of avian brood parasite-host coevolution. *Animal Behavior*, 84, 3–12. <https://doi.org/10.1016/j.anbehav.2012.04.011>
- Fontain, J. J., & Martin, T. E. (2006). Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters*, 9, 428–434. <https://doi.org/10.1111/j.1461-0248.2006.00892.x>
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression*, 3rd ed. Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Gluckman, T.-L., & Mundy, N. I. (2013). Cuckoos in raptors' clothing: Barred plumage illuminates a fundamental principle of Batesian mimicry. *Animal Behavior*, 86, 1165–1181. <https://doi.org/10.1016/j.anbehav.2013.09.020>
- Graham, K. F., & Shutler, D. (2019). How robust are risk-taking associations in incubating birds? A test and a review. *Behavioral Ecology and Sociobiology*, 73, 79. <https://doi.org/10.1007/s00265-019-2692-x>
- Grim, T., Samas, P., Procházka, P., & Rutila, J. (2014). Are tits really unsuitable hosts for the common cuckoo? *Ornis Fennica*, 91, 166–177.
- Hartig, F. (2020). DHARMA: Residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.3.2.0. <https://CRAN.R-project.org/package=DHARMA>
- Honza, M., Šícha, V., Procházka, P., & Ležalová, R. (2006). Host nest defense against a color-dimorphic brood parasite: Great reed warblers (*Acrocephalus arundinaceus*) versus common cuckoos (*Cuculus canorus*). *Journal of Ornithology*, 147, 629–637. <https://doi.org/10.1007/s10336-006-0088-y>
- Jelínek, V., Šulc, M., Štětková, G., & Honza, M. (2020). Fast and furious: Host aggression modulates behaviour of brood parasites. *bioRxiv*, 2020.04.27.063933, 1–15. <https://doi.org/10.1101/2020.04.27.063933>
- Kleindorfer, S., Fessl, B., & Hoi, H. (2005). Avian nest defence behaviour: Assessment in relation to predator distance and type and nest height. *Animal Behavior*, 69, 307–313. <https://doi.org/10.1016/j.anbehav.2004.06.003>
- Krams, I. A., Krama, T., Freeberg, T. M., Krams, R., & Sieving, K. E. (2020). Attacks of songbirds in mixed-species flocks by Eurasian sparrowhawks: Strategies of predators and potential prey. *Journal of Field Ornithology*, 91, 1–8. <https://doi.org/10.1111/jfo.12350>
- Kryštofková, M., Haas, M., & Exnerová, A. (2011). Nest defense in blackbirds *Turdus merula*: Effect of predator distance and parental sex. *Acta Ornithologica*, 46, 55–63. <https://doi.org/10.3161/000164511X589938>
- Lawson, S. L., Enos, J. K., Mendes, N. C., Gill, S. A., & Hauber, M. E. (2020). Heterospecific eavesdropping on an anti-parasitic referential alarm call. *Communications Biology*, 3, 143. <https://doi.org/10.1038/s42003-020-0875-7>
- Lawson, S. L., Leuschner, N., Gill, B. J., Enos, J. K., & Hauber, M. E. (2020). Loss of graded enemy recognition in a whitehead population allopatric with brood-parasitic Long-tailed Cuckoos. *Avocetta*, 44, 3–10. <https://doi.org/10.30456/AVO.2020104>
- Lee, J. W., Kim, H. N., Yoo, S., & Yoo, J. C. (2019). Common cuckoo females may escape male sexual harassment by color polymorphism. *Scientific Reports*, 9, 7515. <https://doi.org/10.1038/s41598-019-44024-6>
- Leisler, B., & Schulze-Hagen, K. (2011). *Reed warblers: Diversity in a uniform bird family*. Leiden, The Netherlands. KNNV Publishing. <https://doi.org/10.1163/9789004278028>
- Lenth, R. (2020). emmeans: Estimated marginal means, aka least-squares means. R Package Version 1.4.6. <https://CRAN.R-project.org/package=emmeans>
- Li, D., Wei, H., Zhang, Z., Liang, W., & Stokke, B. G. (2015). Oriental reed warbler (*Acrocephalus orientalis*) nest defence behaviour towards brood parasites and nest predators. *Behaviour*, 152, 1601–1621. <https://doi.org/10.1163/1568539x-00003295>
- Ma, L., Yang, C., & Liang, W. (2018). Hawk mimicry does not reduce attacks of cuckoos by highly aggressive hosts. *Avian Research*, 9, 35. <https://doi.org/10.1186/s40657-018-0127-4>

- Marton, A., Fülöp, A., Ozogány, K., Moskát, C., & Bán, M. (2019). Host alarm calls attract the unwanted attention of the brood parasitic common cuckoo. *Scientific Reports*, 9, 18563. <https://doi.org/10.1038/s41598-019-54909-1>
- Medina, I., & Langmore, N. E. (2015). Batten down the thatches: Front-line defences in an apparently defenceless cuckoo host. *Animal Behavior*, 112, 195–201. <https://doi.org/10.1016/j.anbehav.2015.12.006>
- Moksnes, A., & Røskft, E. (1988). Responses of fieldfares *Turdus pilaris* and bramblings *Fringilla montifringilla* to experimental parasitism by the cuckoo *Cuculus canorus*. *Ibis*, 130, 535–539. <https://doi.org/10.1111/j.1474-919X.1988.tb02719.x>
- Moksnes, A., Røskft, E., Braa, A. T., Korsnes, L., Lampe, H. M., & Pedersen, H. C. (1991). Behavioural response of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour*, 116, 64–89. <https://doi.org/10.1163/156853990X00365>
- Molnár, B. (1944). The cuckoo in the Hungarian plain. *Aquila*, 51, 100–112.
- Moskát, C. (2005). Nest defence and egg rejection in great reed warblers over the breeding cycle: Are they synchronised with the risk of brood parasitism? *Annales Zoologici Fennici*, 42, 579–586.
- Moskát, C., Elek, Z., Bán, M., Geltsch, N., & Hauber, M. E. (2017). Can common cuckoos discriminate between neighbours and strangers by their calls? *Animal Behavior*, 126, 253–260. <https://doi.org/10.1016/j.anbehav.2017.02.013>
- Moskát, C., & Hauber, M. E. (2019). Sex-specific responses to simulated territorial intrusions in the common cuckoo: A dual function of female acoustic signalling. *Behavioral Ecology and Sociobiology*, 73, 60. <https://doi.org/10.1007/s00265-019-2665-0>
- Moskát, C., Hauber, M. E., Růžicková, J., Marton, A., Bán, M., & Elek, Z. (2020). Female-female aggression and male responses to the two colour morphs of female common cuckoos. *The Science of Nature*, 107, 28. <https://doi.org/10.1007/s00114-020-01680-3>
- Moskát, C., & Honza, M. (2000). Effect of time and nest site characteristics on the risk of cuckoo *Cuculus canorus* parasitism in the great reed warbler *Acrocephalus arundinaceus*. *Ecography*, 23, 335–341. <https://doi.org/10.1111/j.1600-0587.2000.tb00289.x>
- Němec, M., Syrová, M., Dokoupilová, L., Veselý, P., Šmilauer, P., Landová, E., Lišková, S., & Fuchs, R. (2015). Surface texture and priming play important roles in predator recognition by the red-backed shrike in field experiments. *Animal Cognition*, 18, 259–268. <https://doi.org/10.1007/s10071-014-0796-2>
- Newton, I. (1986). *The sparrowhawk*. T. and A. D. Poyser.
- Pavel, V. (2006). When do altricial birds reach maximum of their brood defence intensity? *Journal of Ethology*, 24, 175–179. <https://doi.org/10.1007/s10164-005-0178-y>
- R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Røskft, E., Moksnes, A., Stokke, B. G., Bičík, V., & Moskát, C. (2002). Aggression to dummy cuckoos by potential European cuckoo hosts. *Behaviour*, 139, 613–628. <https://doi.org/10.1163/15685390260136735>
- Schulze-Hagen, K. (1992). Parasitierung und Brutverluste durch Kuckuck (*Cuculus canorus*) bei Teich- und Sumpfrohrsänger (*Acrocephalus scirpaceus*, *A. palustris*) in Mittel- und Westeuropa. *Journal of Ornithology*, 133, 237–249. <https://doi.org/10.1007/BF01645635>
- Sejberg, D., Bensch, S., & Hasselquist, D. (2000). Nestling provisioning in polygynous great reed warblers (*Acrocephalus arundinaceus*): Do males bring larger prey to compensate for fewer nest visits? *Behavioral Ecology and Sociobiology*, 47, 213–219. <https://doi.org/10.1007/s002650050658>
- Soler, M., Pérez-Contreras, T., & Soler, J. J. (2017). Brood parasites as predators: Farming and mafia strategies. In Soler, M. (Ed.), *Avian brood parasitism: Behaviour, ecology, evolution and coevolution* (pp. 271–286). Springer International Publishing. https://doi.org/10.1007/978-3-319-73138-4_15
- Strnad, M., Nimec, M., Veselý, P., & Fuchs, R. (2012). Red-backed shrikes (*Lanius collurio*) adjust the mobbing intensity, but not mobbing frequency, by assessing the potential threat to themselves from different predators. *Ornis Fennica*, 89, 206–215.
- Šulc, M., Štětková, G., Procházka, P., Požgayová, M., Sosnovcová, K., Studecký, J., & Honza, H. (2020). Caught on camera: Circumstantial evidence for fatal mobbing of an avian brood parasite by a host. *Journal of Vertebrate Biology*, 69, 1–6. <https://doi.org/10.25225/jvb.20027>
- Thorogood, R., & Davies, N. B. (2012). Cuckoos combat socially transmitted defenses of reed warbler hosts with a plumage polymorphism. *Science*, 337, 578. <https://doi.org/10.1126/science.1220759>
- Trivers, L. R. (1974). Parent-offspring conflict. *American Zoologist*, 14, 249–264. <https://doi.org/10.1093/icb/14.1.249>
- Trnka, A., & Grim, T. (2013). Color plumage polymorphism and predator mimicry in brood parasites. *Frontiers in Zoology*, 10, 25. <https://doi.org/10.1186/1742-9994-10-25>
- Trnka, A., & Prokop, P. (2010). Does social mating system influence nest defence behaviour in great reed warbler *Acrocephalus arundinaceus* males? *Ethology*, 116, 1075–1083. <https://doi.org/10.1111/j.1439-0310.2010.01821.x>
- Trnka, A., & Prokop, P. (2012). The effectiveness of hawk mimicry in protecting cuckoos from aggressive hosts. *Animal Behavior*, 83, 263–268. <https://doi.org/10.1016/j.anbehav.2011.10.036>
- Trnka, A., Prokop, P., & Grim, T. (2012). Uncovering dangerous cheats: How do avian hosts recognize adult brood parasites? *PLoS ONE*, 7, e37445. <https://doi.org/10.1371/journal.pone.0037445>
- Trnka, A., Trnka, M., & Grim, T. (2015). Do rufous common cuckoo females indeed mimic a predator? An experimental test. *Biological Journal of the Linnean Society*, 116(1), 134–143. <https://doi.org/10.1111/bij.12570>
- Tryjanowski, P., Morelli, F., Kwiecieński, Z., Indykiewicz, P., & Møller, A. P. (2018). Birds respond similarly to taxidermic models and live cuckoos *Cuculus canorus*. *Journal of Ethology*, 36, 243–249. <https://doi.org/10.1007/s10164-018-0554-z>
- Welbergen, J. A., & Davies, N. B. (2011). A parasite in wolf's clothing: Hawk mimicry reduces mobbing of cuckoos by hosts. *Behavioral Ecology*, 22, 574–579. <https://doi.org/10.1093/beheco/arr008>
- Wyllie, I. (1981). *The cuckoo*. Batsford.
- Xia, C., Deng, Z., Lloyd, H., Møller, A. P., Zhao, X., & Zhang, Y. (2019). The function of three main call types in common cuckoo calls. *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. *Nature Ecology and Evolution*, 1, 1520–1525. <https://doi.org/10.1038/s41559-017-0279-3>
- Yu, J., Lu, H., Sun, W., Liang, W., Wang, H., & Møller, A. P. (2019). Heterospecific alarm-call recognition in two warbler hosts of common cuckoos. *Animal Cognition*, 22, 1149–1157. <https://doi.org/10.1007/s10071-019-01307-9>
- Zhang, L., Liu, J., Zhang, H., Wan, D., Liang, W., & Møller, A. P. (2020). Fight or flight? Geographic variation in antipredator defenses by cinereous tits. *Global Ecology and Conservation*, 24, e01207. <https://doi.org/10.1016/j.gecco.2020.e01207>
- Zölei, A., Bán, M., & Moskát, C. (2015). No change in common cuckoo *Cuculus canorus* parasitism and great reed warblers' *Acrocephalus arundinaceus* egg rejection after seven decades. *Journal of Avian Biology*, 46, 570–576. <https://doi.org/10.1111/jav.00673>

How to cite this article: Marton A, Fülöp A, Bán M, Hauber ME, Moskát C. Female common cuckoo calls dampen the mobbing intensity of great reed warbler hosts. *Ethology*. 2021;127:286–293. <https://doi.org/10.1111/eth.13126>