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Birds respond similarly to taxidermic models and live cuckoos *Cuculus canorus*

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Abstract

Stuffed birds are widely used in research for identifying effects of predators and nest parasites on bird behaviour, studying levels of aggression and the size of territories. However, the fact that these models do not move or vocalize may question the results of such studies and open them to criticism. One solution would be to determine how the results of research using stuffed dummies correlate with the response of wild animals to enemies under the same environmental conditions. In a first attempt, we examined the correlation between the intensity of mobbing of a dummy cuckoo *Cuculus canorus* and interactions with live cuckoos in the field during the breeding season in western Poland. A total of 39 bird species mobbed cuckoo dummies; all 39 were found to attack live cuckoos, while 24 species (61.5%) did so during experiments using a dummy. The number of individual birds involved in mobbing a dummy was positively correlated with the number of individuals attacking real cuckoos in the same areas, even when the most commonly mobbing species, the barn swallow *Hirundo rustica*, was excluded from the analyses. However, we did not find significant differences in frequency of mobbing behaviour depending on cuckoo behaviour described as flight or sitting, or calling rather than remaining quiet. Therefore, we conclude that the use of a dummy for studying mobbing of hosts and non-hosts of the cuckoo provide results that are similar to those made in response to the behaviour of live hosts.

Keywords Anti-parasite behaviour · Cuckoo · *Cuculus canorus* · Mobbing

Introduction

Dummies and stuffed birds are widely used in the study of mobbing of predators (Curio et al. 1978; Suzuki and Ueda 2013; Syrová et al. 2016) and brood parasites, including the common cuckoo *Cuculus canorus* (Moksnes et al. 1991; Røskaft et al. 2002; Grim 2005). Use of this method produced large amounts of valuable information on predator detectability (Syrová et al. 2016), brood parasite detectability (McLean 1987; Dyrz and Hałupka 2006), cognitive ability (Beránková et al. 2014) and many other kinds of behaviour connected with territory size and borders (Curio et al. 1978; Knight and Temple 1986). This method has been commonly used since early studies in quantitative ethology (Altmann 1956; Melzack et al. 1959; Curio et al. 1978). The method is assumed to function well in studies of brood parasitism and allow discrimination between cuckoos and predators, like the sparrowhawk *Accipiter nisus* and kestrel *Falco tinnunculus* (Trnka et al. 2012; Gluckman and Mundy 2013), and even allow discrimination between particular

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raptor species (e.g. Soard and Ritchison 2009, Courter and Ritchison 2010).

Although dummies are often used, this method is only useful if validated in the field. However, it has often been confirmed that the method works and that birds attack cuckoo dummies. However, the only test that validates the use of dummies and the response to live cuckoos in the field was reported by Liang and Møller (2015). In situations when there are no explicit tests of whether the presentation of dummies reflects the situation in the field, criticism against the reliability of the use of dummies can be raised and interpretations should be made with caution. First, it is an artificial situation to make tests using a dummy, which mainly remains immobile and silent, as revealed by birds reacting more strongly to flying objects (Schleidt et al. 2011). Birds can discriminate between live and artificial objects and subsequently modulate behaviour (Scriba and Goymann 2008). Moreover, birds may mob an enemy in particular situations as, for example, when flying or sitting and defending a territory (Curio et al. 1978; Syrová et al. 2016). For example, cuckoos may change behaviour while searching for nests of hosts, when vocalizing and when interacting with conspecifics (Teuschl et al. 1998; Møller et al. 2016; Yu et al. 2016; Moskát et al. 2017). Sometimes the reaction of birds to dummies is used to distinguish between the relative importance of particular species such as nest predators or brood parasites, and classically a pigeon is used as a control (reviewed by Grim 2005). However, another way of avoiding criticism is to use as a control dummy an object similar to the tested animal, for example a cuckoo that may influence the results of an experiment leading to erroneous conclusions (Grim 2005). These reflections raise the question of whether experiments with dummies resemble the real situation with live birds in the field.

To address this question, we investigated whether the reaction of birds to a cuckoo dummy in playback experiments reflected the situation for live vocalizing cuckoo males in the field. Here we correlated mobbing against a brood parasite and a dummy, both in experiments and during field observations of live cuckoos. We predicted that if the use of a dummy was reliable in a particular study of the response of a given bird species to a brood parasite, we should find a strong positive correlation between level of aggression in response to a dummy and in the field to live cuckoos. Additionally, we analyzed how bird species reacted to the behaviour of cuckoos (flying vs sitting and calling vs being silent). Such differences in behaviour may provide information relevant for the design of experiments that may better simulate field conditions.

Materials and methods

Study area

The field study was conducted during late April–late June 2016 in Wielkopolska province, western Poland (52°N, 16°E). Information on the density of cuckoos and potential hosts is reported in Tryjanowski and Morelli (2015). Data were collected in two ways: (1) experimentally using a cuckoo dummy shown together with playback; and (2) by observation of the reaction of birds to live cuckoos recorded in the field.

Dummy experiments

We simulated natural conditions of cuckoo males in the field by using stuffed cuckoo males (four different individuals from museums). A stuffed cuckoo was provided on a 2.5-m wooden pole. The pole with a stuffed cuckoo was visible, because it was provided at the edge of shrubs, tree clumps, on the bank of small water bodies or on a fence at the edge of a village. The cuckoo was not searching for potential nests of the host species. The dummy was accompanied by a loudspeaker (placed on the slat under the dummy) for playing back cuckoo calls (5 and 50 cu-coo syllables), reflecting the real situation in the field (Møller et al. 2016) to test the importance of call duration, female presence, and time of the breeding season (Tryjanowski, Møller, and Morelli in prep.). To avoid problems with pseudoreplication and potential preferences for the call of a particular male (e.g. Jung et al. 2014), we used synthetic calls of cuckoos prepared with Avisoft SASLab Pro 5.2 (Specht 2016). The synthetic calls were prepared based on their natural equivalent in the following steps: (1) creation of a sonogram, (2) scanning of frequency contour and amplitude envelope, and (3) saving a WAV file. For scanning we used automatic three-threshold element separation and appropriate threshold relative to the maximum signal amplitude. Synthetic calls were very similar acoustically, visually and when compared with calls produced by live cuckoos.

Synthetic calls were pasted into WAV files prepared for broadcasting during experiments. Broadcast sounds began with 60 s of silence, which allowed the observer to set up the loudspeaker and recede to a standard distance of 100 m from the loudspeaker before start of playback. After 60 s the loudspeaker reproduced synthetic calls of two variants: short duration (5 cuckoo calls during 6 s plus 54 s silence) repeated 5 times, and long duration (25 cuckoo calls during 35 s plus 25 s of silence), repeated 5 times. Calls were broadcast with a waterproof Creative MUVO mini[®] loudspeaker and amplitude was standardized for all playbacks.

Experimental data with dummy and playback were collected during 1 May–15 June 2016 in the morning (6:00–9:30) on days with no rain or strong wind.

Field observations

Simultaneously with the experiments with playback and in the neighboring area (radius 10 km) during follow-up of the experiments, but also on other days, when PT, PI and ZK were searching for additional sites for potential experiments, the same observers recorded responses of birds to live cuckoos. This part of the field work was conducted during 29 April–30 June 2016. This approach allowed collection of data used for analyzing the correlation between data obtained from field observations and playback experiments.

Similar to the method described by Liang and Møller (2015), observed cuckoos were classified as flying or sitting, but observers also paid special attention to whether the cuckoo was calling or silent. Although data were collected at a large spatial scale, we cannot be sure that observations always represented different individuals, just as in other studies of unbanded cuckoos (Welbergen and Davies 2008, 2009; Trnka and Grim 2013; Moskát et al. 2017) and, moreover, more detailed study using radio-transmitters suggested local fidelity (Vogl et al. 2004). Therefore, only the first attack in a particular area (defined as a circle with a radius of 1 km) was included in the analyses to avoid pseudoreplication, excluding situations when more cuckoos were observed simultaneously).

PT, ZK and PI quantified the abundance of the local breeding bird community by recorded birds at 184 points at a distance of 100 m from each calling cuckoo and each dummy presentation. Birds were counted using the point-count method with 5-minute observations without repetition (Blondel et al. 1970), and then used to describe the breeding bird community in the study area.

Statistical analysis

In order to avoid errors when recording interactions between cuckoos and other species of birds (nervous behaviour, changes in song pattern) the response of birds to the model cuckoo was included only if the birds physically attacked the dummy cuckoo (mobbing). Similarly, during field observations of live cuckoos only mobbing reactions directed towards the cuckoo were used for analyses. We paid special attention when cuckoos were attacked by other birds, and due to the situation in the field we divided all situations into four categories of cuckoo behaviour: (1) sitting and no calling; (2) flying and no calling; (3) sitting and calling; and (4) flying and calling. Only species recorded at least once (in playback experiments mobbing or during observations of interactions with live cuckoos) were included in

the analyses. Hosts of cuckoos were ranked according to the frequency of parasitism of different species in Poland (Wesolowski and Mokwa 2013), the only available data for Poland, but it is worth noting that the use of particular bird species is dynamic and changed temporally in accordance with the arms race hypothesis (Lovász and Moskát 2004).

We used generalized linear models (GLM) to investigate the association between number of individuals involved in mobbing the dummy and number of individuals observed in the same area mobbing live cuckoos. Models were performed using the ‘lme4’ package for R (Bates et al. 2014). The number of individuals mobbing the dummy was modelled as a response variable, assuming a Poisson distribution for this count variable. The covariates were number of individuals attacking live cuckoos, abundance of each species of bird and the interaction between the two variables. The incorporation of abundance of birds in the model can remove any problem related to the possibility of detecting a high rate of attacks just for density-dependent reasons (for instance if abundant species are expected to be found more often attacking both live and dummy cuckoos).

The standardized estimates were obtained using the ‘QuantPsyc’ package for R (Fletcher 2015). All statistical tests were performed with R software (R Development Core Team 2017).

Results

In total, among cuckoo mobbers, 39 bird species and 181 individuals were recorded during the study (Table 1). All species were recorded during observations in the field interacting with live cuckoos, and 24 of them (61.5%) attacked the dummy during experiments. A total of 89 and 92 individual birds were recorded during observations and playback experiments, respectively. In total in the field the cuckoo was observed in 315 cases, and in 89 cases (27.6%) it was mobbed by other species. However, the frequency of mobbing was not significantly related to four types of cuckoo behaviour: (1) sitting and no calling; (2) flying and no calling; (3) sitting and calling; and (4) flying and calling (Pearson chi-square = 1.63, $df = 1, 3$, $P = 0.202$).

There was a significant positive correlation between the number of individuals per species involved in mobbing in experiments with the dummy and observed in the same area attacking live cuckoos (Fig. 1a). Even excluding the barn swallow *Hirundo rustica*, because this bird species responded much more strongly than predicted (see Fig. 1a), we found a significant positive correlation between the number of individuals responding to live cuckoos and the number of individuals responding to dummy cuckoos (Table 1; Fig. 1b). The relative abundance of each bird species and the

Table 1 Species noted to react to a live cuckoo in the field and to a dummy during dummy presentation experiments

Species	Live cuckoo	Dummy
<i>Acrocephalus palustris</i>	2	2
<i>Acrocephalus schoebaneus</i>	1	1
<i>Alauda arvensis</i>	1	0
<i>Anthus pratensis</i>	1	1
<i>Apus apus</i>	1	0
<i>Carduelis carduelis</i>	1	0
<i>Chloris chloris</i>	1	0
<i>Corvus cornix</i>	3	1
<i>Cyanistes cyaneus</i>	2	3
<i>Delichon urbicum</i>	3	4
<i>Emberiza citrinella</i>	3	3
<i>Erithacus rubecula</i>	2	1
<i>Fringilla coelebs</i>	2	0
<i>Hippolais icterina</i>	1	0
<i>Hirundo rustica</i>	15	50
<i>Lanius collurio</i>	4	2
<i>Lanius excubitor</i>	1	0
<i>Motacilla alba</i>	6	2
<i>Motacilla flava</i>	4	1
<i>Muscicapa striata</i>	1	1
<i>Oriolus oriolus</i>	3	0
<i>Parus major</i>	5	9
<i>Passer domesticus</i>	2	1
<i>Passer montanus</i>	1	1
<i>Phoenicurus ochruros</i>	1	0
<i>Phylloscopus collybita</i>	1	2
<i>Phylloscopus trochilus</i>	1	1
<i>Pica pica</i>	3	0
<i>Picus viridis</i>	1	0
<i>Riparia riparia</i>	1	1
<i>Serinus serinus</i>	1	0
<i>Sturnus vulgaris</i>	4	1
<i>Sylvia atricapilla</i>	2	2
<i>Sylvia communis</i>	1	1
<i>Sylvia curruca</i>	1	1
<i>Sylvia nisoria</i>	1	0
<i>Turdus merula</i>	1	0
<i>Turdus pilaris</i>	3	0
<i>Upupa eppops</i>	1	0
Total	89	92

interaction with the number of attacks were not significantly related to the response (Table 2).

However, if the number of cases of brood parasitism for each species in Poland was controlled statistically, the correlation between the number of individuals responding to live cuckoos and the number of individuals responding to dummy cuckoos was even more strongly positive and

highly significant (partial correlation: $r_p = 0.791$, $df = 38$, $P = 0.001$).

Discussion

Although data were obtained in not experimentally controlled conditions, focused mainly on cuckoo males and hence may have some limitations, we found interesting results well worth discussion. We also note that data were collected during the entire breeding season, and we did not search for nests, so we had no information on the nesting stages when the potential hosts mobbed live or stuffed cuckoos. Hosts may show similarly high levels of aggression toward the cuckoo from laying to the nestling period, although that has not been fully confirmed (Moskát 2005). However, the bias applied to both methods, dummies and natural cuckoos. Firstly, we found a strong positive correlation between the intensity of mobbing in playback experiments and observations in the field of live cuckoos. Moreover, this response was stronger for hosts than for non-hosts. However, due to limited sample size, e.g. number of attacks, only one particular case was suitable for analysis, the barn swallow. Liang and Møller (2015) showed that barn swallows reacted as strongly towards dummies as to live cuckoos. Here, we also found that barn swallows mobbed the dummy much more strongly than predicted from field observations of live cuckoos. The barn swallow is known to intensely mob enemies including cuckoos (Møller 1987; Brown and Hoogland 1986; Liang and Møller 2015; Yu et al. 2016). Why are barn swallows so aggressive towards dummies? Liang and Møller (2015) compared attacks on dummies and live cuckoos in China, where the barn swallow is often host of cuckoo. Perhaps the response by barn swallows to dummies is so strong because dummies ‘behave’ in a way that a live cuckoo would not. Live cuckoos may communicate with hosts, while dummies continue to behave in a way that hosts may consider to be an escalation. Alternatively, barn swallows may consider cuckoos to not only be brood parasites (which is rare in Europe), as documented especially in older studies (Moksnes and Røskoft 2009), but barn swallows may also visually confuse cuckoos with sparrowhawks (Trnka et al. 2012; Gluckman and Mundy 2013; Lyon and Gilbert 2013).

We used a stuffed dummy supplemented with a loud-speaker that played back the call of a cuckoo. This created a different situation from the exclusive use of a silent dummy (Moksnes et al. 1991, 2000; Dyrce and Hałupka 2006). Therefore, bird responses to live cuckoos did not depend on whether the cuckoo flew or sat, if the key element was the call. Similar reactions to dummies were also reported in studies of predation (e.g. Cockrem and Silverin 2002), and

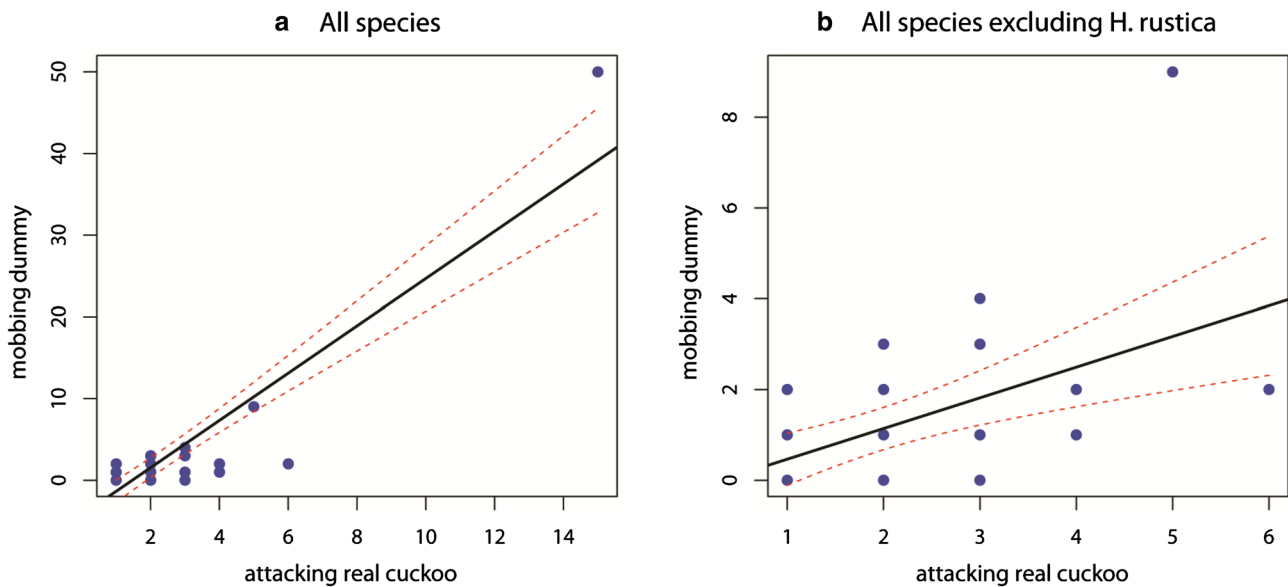


Fig. 1 Correlation between number of bird individuals of each species that attacked a cuckoo (*x*-axis) in the field and in experimental trials during presentation of a dummy (*y*-axis) for all species com-

bined (**a**), and when the barn swallow *Hirundo rustica* was excluded (**b**). The *lines* are the linear regression lines and the 95% confidence intervals

Table 2 Generalized linear model, accounting for association between number of individuals involved in attacks on dummy and number of individuals attacking live cuckoos and the relative abundance of each bird species in the same study area

Predictors	Estimate	CI	SE	<i>z</i>	<i>P</i>
Intercept	− 0.782	− 1.644/0.017	0.308	− 3.1	0.0641
Attacks on live cuckoo	0.324	0.172/0.642	0.119	3.4	0.0006
Bird species abundance	− 0.329	− 0.678/0.259	0.237	− 0.6	0.5709
Attacks on live cuckoo × bird species abundance	0.023	− 0.074/0.167	0.061	0.5	0.6346

The table shows standardised estimates, 95% confidence intervals (CI), SE, *z* and *P*

this was already suggested for the study of cuckoos (Grim 2005).

Another possibility rather than using both a dummy and a loudspeaker with cuckoo calls is to use more advanced technology, such as mobile models which can produce calls interactively (e.g. Reĸ and Magrath 2016). Recently, even ‘robo-raptor’ models have been used as a powerful tool for providing increased realism in simulated predator encounters without sacrificing experimental control (Carlson et al. 2017). Such models have so far never been used with cuckoos.

In summary, the use of stuffed cuckoo dummies combined with calls caused responses by birds similar to those

produced in response to live cuckoos. Cuckoos are recognised by other bird species, and hence the present study confirms the value of using this simple, but efficient and reliable study method (Grim 2005; Liang and Møller 2015).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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