ANIMAL BEHAVIOUR

The effectiveness of hawk mimicry in protecting cuckoos from aggressive hosts

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The close resemblance between the common cuckoo, Cuculus canorus, and the Eurasian sparrowhawk, Accipiter nisus, is often viewed as Batesian mimicry evolved by the cuckoo in response to the aggression of its host. However, the effectiveness of such mimicry is poorly known. We examined cuckoo–hawk discrimination ability in the great reed warbler, Acrocephalus arundinaceus, a well-known and aggressive cuckoo host. We measured the responses of birds to three combinations of simultaneously presented taxidermic mounts of the cuckoo, sparrowhawk and turtle dove, as a harmless control, placed near their nests. Great reed warblers clearly discriminated the two enemies from the innocuous species. They always attacked cuckoos and sparrowhawks more often than turtle doves suggesting they considered both a danger to their broods. However, when we confronted the tested birds with the simultaneously presented mounts of these species, the parents attacked the cuckoo more frequently than the sparrowhawk. The results revealed that although great reed warblers attacked both cuckoo and sparrowhawk mounts near their nest, they were able to discriminate between them. This may suggest that if cuckoos had evolved the visual mimicry of a sparrowhawk to avoid host attacks, this mimicry may be unsuccessful not only because it is imperfect and hosts can learn to discriminate but also because of the generalized nest defence of more aggressive hosts.
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In the coevolutionary arms race between brood parasites and their hosts, a variety of unique adaptations and counteradaptations have evolved on both sides at all host nesting stages (Rothstein & Robinson 1998; Langmore et al. 2003; Grim 2005b; Krüger 2007). The most effective defence against brood parasitism is preventing parasitic females from laying eggs in a host nest (Welbergen & Davies 2009; Langmore & Kilner 2010). Many host species have therefore evolved the capability to recognize parasitic adults near their nests as a special threat and respond to them more aggressively or in different ways than they respond to other species (Duckworth 1991; Gill et al. 1997; Grim 2005a; Welbergen & Davies 2008; Campobello & Sealy 2010). Such defensive behaviour on the part of hosts, however, inflicts direct or indirect costs on brood parasites (Welbergen & Davies 2009). Thus, selection should favour parasite counteradaptations that would reduce the probability of being detected or attacked by hosts. Recent studies suggest that such adaptations, apart from cryptic laying (Davies & Brooke 1988), may also be the visual mimicry of small raptors by brood parasites (Davies & Welbergen 2008; Welbergen & Davies 2011). The most

well-known example of such mimicry is the common cuckoo, Cuculus canorus (hereafter the cuckoo), which is, at least from a human perspective, similar in size, shape, plumage and flight to the Eurasian sparrowhawk, Accipiter nisus (hereafter sparrowhawk, Duckworth 1991; Davies & Welbergen 2008).

Cuckoos and sparrowhawks generally pose different kinds of threats to birds. While cuckoos are a threat only to host nests (as brood parasites or nest predators, Alvarez 1994; Kim & Yamagishi 1999; Moksnes et al. 2000; Welbergen & Davies 2008), sparrowhawks are highly specialized predators of adult passerines (Götmark & Post 1996). Thus, cuckoo–hawk mimicry should make the parasite appear dangerous to adult hosts and, consequently, reduce their aggression (Davies & Welbergen 2008). Therefore, it is also generally assumed that cuckoo–hawk mimicry has probably evolved in response to mobbing by hosts (Welbergen & Davies 2009; Langmore & Kilner 2010). However, given that the cuckoo does not mimic the sparrowhawk perfectly, as it lacks certain important features of raptors, such as hooked beak and claws, and its hosts can learn to discriminate between enemies, the effectiveness of such mimicry is still questionable (see for example Duckworth 1991; Lindholm & Thomas 2000; Welbergen & Davies 2011). The fact that cuckoos, despite some host recognition, may still gain advantage from the sparrowhawk resemblance, has been demonstrated in only one host species, the reed warbler,

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Acrocephalus scirpaceus (Welbergen & Davies 2009, 2011), which is, in general, less aggressive towards all intruders near the nest than many other cuckoo host species, and only rarely contact-attacks them (Duckworth 1991; Lindholm & Thomas 2000; Røskaft et al. 2002; Dyrcz & Halupka 2006; Campobello & Sealy 2010). However, as birds vary greatly in their aggressiveness and willingness to put themselves at risk when defending their nests against potential nest predators (Montgomerie & Weatherhead 1988), the results of previous studies cannot be generalized for all host species. Thus, if we want to demonstrate that cuckoo–hawk resemblance truly reduces the risk of being attacked by hosts, we also need to test how this mimicry is effective against more aggressive host species that regularly attack intruders near their nest. If such hosts behave as warily towards cuckoos as towards sparrowhawks and they do not attack them directly, then the cuckoo–hawk mimicry can be considered effective.

We examined the effectiveness of cuckoo–hawk mimicry for the great reed warbler, *Acrocephalus arundinaceus*, a well-known and aggressive cuckoo host in Central Europe (Moksnes et al. 1990; Moskát 2005; Dyrcz & Halupka 2006), with well-developed adaptations against brood parasitism (Bártol et al. 2002; Požgayová et al. 2009) indicating a long coevolutionary history with this brood parasite. We used taxidermic mounts of a cuckoo, a sparrowhawk and a turtle dove, *Streptopelia turtur*, as a harmless control, placed in three different dyads near the nest. The main aim of this study was to determine whether great reed warblers are able to discriminate between a cuckoo and a sparrowhawk and how aggressive they are against the two enemies. As great reed warblers are highly aggressive towards any type of intruder near their nest (Kleindorfer et al. 2005; Trnka & Prokop 2010), including the cuckoo (Bártol et al. 2002; Požgayová et al. 2009) and the sparrowhawk (Honza et al. 2010), we predicted that (1) they would attack both cuckoo and sparrowhawk mounts and, thus, cuckoo–hawk mimicry is not effective against this species in terms of protecting the cuckoos from host attacks. Given that the nest defence behaviour of birds should vary with the threat that a particular nest intruder represents (Kleindorfer et al. 2005; Tvardíková & Fuchs 2010), we also predicted that (2) if great reed warblers discriminate between cuckoos and sparrowhawks, then the intensity of the nest defence against the cuckoo mount would be higher at the end of the egg-laying stage, when brood parasites pose the greatest threat to the parents, than at the late nestling stage (but see Moskát 2005), while aggressive responses to the sparrowhawk, which preys almost exclusively on adult birds (Cramp & Simmons 1980), should be similar at both nesting stages. Thus, cuckoo–hawk discrimination should be more pronounced at the end of the egg-laying stage than the late nestling stage.

METHODS

Study Site and Species

The study was carried out in a fishpond system near Štúrovo, southwestern Slovakia in 2009 and 2010. Great reed warbler nests were found in narrow strips of the reeds fringing the ponds. The study population consists of 40–60 pairs. The nest predation rate averages 20% (our own unpublished data). There is also known intraspecific nest predation (infanticide) in this species whereby lower-ranking females destroy eggs of high-ranking females to gain increased paternal investment (Hansson et al. 1997; Trnka et al. 2010). The most frequent predators of great reed warbler nests in the study area are the little bittern, *Ixobrychus minutus*, and the marsh harrier, *Circus aeruginosus*. The sparrowhawk, in contrast, has never been observed in the study area during the great reed warbler breeding season. It occurs at ponds only occasionally in the

winter. The nearest breeding spots of this raptor are about 2–5 km from the study ponds and its density reaches two or three breeding pairs/100 km^2 (our own unpublished data). The mean rate of cuckoo parasitism averaged 31%, while the annual rate of successful parasitism ranges from 16% to 20% (Trnka & Prokop 2011).

In April, soon after the arrival of great reed warblers from the African wintering grounds, we mist-netted 118 adult birds in the study area in 2009 and 2010, which represents (based on our observations) about 90% of all birds present in the ponds. We used tape recordings of conspecific song to attract them to the nets. All the tested birds were individually marked with both aluminium and colour rings. Licences and permission to ring the birds were provided by the Ministry of Environment of the Slovak Republic.

Discrimination Treatments

Cuckoo–hawk discrimination in the great reed warbler was studied by using taxidermic mounts of cuckoos, sparrowhawks (females) and turtle doves. The latter species is similar in size to the cuckoo and was chosen as a control because it does not threaten adult birds or their eggs or young and prefers different habitats. Thus, there is no confounding effect of competition for food or the nest site (see also Grim 2005a). However, the turtle dove is not unknown to the great reed warbler in our study area, because it commonly occupies shrubs growing along the banks of study ponds and also frequently flies over the great reed warbler territories. Moreover, doves and pigeons have also been used in other studies on nest defence in this and other related species (Campobello & Sealy 2010; Honza et al. 2010; Welbergen & Davies 2011). As host defence behaviour may be modified by positive reinforcement and loss of fear when placing single mounts of similar-looking intruders successively (Knight & Temple 1986; Čapek et al. 2010), we followed the experimental procedure used by Ligon & Hill (2009) who simultaneously presented different combinations of dyads of taxidermic mounts. Moreover, because great reed warblers attack the mounts of both cuckoos and sparrowhawks at the highest levels of aggression (Moskát 2005; Honza et al. 2010), this procedure also enabled us to determine the primary target of the host attack (expressed as the number of contact-attacks). The mounts were in life-like positions with folded wings and with their heads pointing forwards. We used two different mounts of each species to reduce the possibility that differences between treatments could be caused by a particular mount. We randomly chose which mount to use at a nest (see Hurlbert 1984). Because great reed warblers frequently strike the occipital area of the skull (Dyrcz & Halupka 2006; own observations), the heads of all the mounts were protected with a thin inconspicuous wirework of the same size and colour to keep the same visibility conditions. In our preliminary study (A. Trnka, unpublished data), the responses of great reed warblers to the mounts of the cuckoo and sparrowhawk with wirework were similar to those to the mounts without wirework. None of the mounts used in the experiment had been destroyed or damaged. Moreover, before each trial the mounts were preened by an experienced taxidermist (the first author). In treatment 1, the mounts of the cuckoo were paired with the mounts of the sparrowhawk, in treatment 2, the mounts of the cuckoo were paired with the mounts of the turtle dove and in treatment 3, the sparrowhawk mounts were paired with the turtle dove mounts. In each treatment, the mounts were placed 0.5 m from the nest at the same height, facing the rim, and 0.8 m from each other. The side on which the mounts were presented was randomized. The space around each nest was arranged to provide the nest owners with a good view of both mounts. Each great reed warbler pair was tested twice, each time with one of three different combinations of dyads of taxidermic mounts. The first test was conducted during

the late egg-laying stage and the second one, in which the combination of dyads was altered, during the late nestling stage. Thus, the same pair was not tested twice with the same dyad of mounts. Great reed warbler individuals were identified by individual colour ring markings. The treatments during the late egg-laying stage were actually conducted 1 or 2 days after clutch completion (great reed warblers lay three to six eggs in our study population, mean $\pm$ SE = 3.58 $\pm$ 0.12, $N = 55$), so as to not disturb the females during egg laying which could lead to nest desertion. In addition, as previous experience of brood parasitism could modify the birds' nest defence behaviour (Čapek et al. 2010) and consequently influence the results of our treatments, we had to make sure that none of the nests tested had been previously parasitized by cuckoos. Therefore, given that cuckoo females lay their eggs in host nests during the host's egg-laying period (Davies & Brooke 1988), we checked each nest daily during the entire laying period for signs of cuckoo parasitism. The treatments during the late nestling stage were performed when the nestlings were 10–12 days old. Of 128 tests, 107 (83.6%) were successful. Results from the other tests could not be included in the analyses because in these cases the tests were broken off and had to be finished prematurely for various reasons (birds were disturbed by researchers, one of the mounts fell in the water, etc.). In total, 55 great reed warbler pairs (19 in 2009 and 36 in 2010) were tested during the egg-laying stage and 52 (18 in 2009 and 34 in 2010) during the late nestling stage (46 of them at the same nest and nine at another replacement nest). None of the birds tested in 2009 were tested again in 2010. The cuckoo–hawk treatment was performed on 44 nests, the cuckoo–dove treatment on 34 nests and the hawk–dove treatment on 29 nests. None of the nests were abandoned or depredated in the first 2 days after the treatment was carried out.

Observations were made from a blind affording a good view of both mounts, placed 5 m from the nest. One observer recorded great reed warbler responses to one mount and another to the second mount. Most of the trials were also videotaped with a digital video camera (Sony DCR-HC17E) and the results compared with the field observations. As the birds were expected to attack all the mounts, we quantified the aggressive behaviour of great reed warblers against each type of mount by counting the contact-attacks (striking and pecking) on a particular mount and expressing this as a frequency. This enabled us to label one mount the winner (receiving more attacks) and so determine the primary target of attacks of the defending parents. Each trial began at the moment of the first contact-attack of one of the parents and lasted 1 min when the mounts were immediately removed to prevent them from being damaged.

Statistical Analysis

Differences in the absolute numbers of attacks on each type of mount within each stage separately (a dependent variable) were compared with the Wilcoxon signed-ranks test. To compare differences in attacks with respect to the treatment, the nesting stage and their interactions, and because most great reed warbler pairs were tested twice, once in the late egg-laying stage and once in the late nestling stage, we employed a generalized linear mixed model (GLMM) with Poisson distribution with the number of attacks towards each individual mount per test as the dependent variable and the great reed warbler breeding pair as a random factor. As fixed factors, the treatment, the species of the target individual mount (type of mount attacked), nesting stage and interactions between stage, type of mount attacked and treatment were used. We determined the best-fit model based on Akaike's information criterion (AIC), corrected for low sample size (AIC$_c$), following the recommendations of Burnham & Anderson (2002).

Models were ranked from the best to the worst and the Akaike weights (w_i) were calculated to give the relative support for a given model compared with the others. For the top candidate models that received substantial support (($AIC_{c(i)} - AIC_{c(min)}) = 2$), we applied model averaging to identify the relative importance of each model term in predicting the response variable and to estimate effect sizes of the predictors. Model selection and averaging procedures were done in the package MuMIn. All calculations were performed in R 2.13.1 (R Development Core Team 2011). Differences in the absolute numbers of attacks on particular types of mount were compared with the Mann–Whitney U test. The proportion of first attacks between males and females was examined separately with a binomial test. The trials in which both parents attacked the mounts simultaneously were removed from this analysis. The sex of specimen first attacked was coded (female = 1, male = 0) and then calculated with a binomial test. All the statistical tests were two tailed and means are presented with SEs.

RESULTS

General Responses

The number of attacks (strikes and pecks) on mounts during a single trial ranged from five to 67. In almost all the trials, both male and female great reed warblers attacked some of the mounts (99/107). Most of the attacks were initiated by one of the parents (72 versus 35 cases), most frequently by females (65 versus 7 cases, binomial test: $P < 0.001$). The birds repeatedly struck the target mount making distress calls, perched on its head and pecked at it. In 11 of 107 trials, another conspecific also participated in the attacks.

Enemy Recognition

In treatments 2 and 3, the mounts of the cuckoo and the sparrowhawk were attacked significantly more frequently than the mount of the turtle dove, in both the late egg-laying and the late nestling stages (Fig. 1, Table 1). However, when we confronted the nest owners with simultaneously presented mounts of the cuckoo and sparrowhawk (treatment 1), the great reed warblers attacked the cuckoo mount significantly more frequently than the sparrowhawk mount, of which they were more wary (Fig. 1, Table 1).

Effects of Treatment and the Nesting Stage

Two top candidate models received substantial support (i.e. ($AIC_{c(i)} - AIC_{c(min)}) = 2$). The best model included treatment, stage, mount attacked, and the interaction between stage and mount attacked. Model averaging showed that all these four terms were important predictors of host aggression (all 95% confidence intervals, CI, of their model-averaged estimates did not include zero; Table 2). The second top model included also the interaction between the mount attacked and treatment, but the 95% CI of its model-averaged estimate contained zero

Cuckoos were attacked in the late egg-laying stage more than in the late nestling stage (Mann–Whitney test: $U = 401$, $N_1 = 41$, $N_2 = 37$, $P < 0.001$), and differences in attacks on sparrowhawks and turtle doves were not or only marginally significant ($U = 574$, $N_1 = 37$, $N_2 = 36$, and 360, $N_1 = 32$ and $N_2 = 31$, $P = 0.309$ and 0.049, respectively). Cuckoos and sparrowhawks received significantly more attacks than turtle doves ($U = 461$, $N_1 = 78$, $N_2 = 63$ and 1179.5, $N_1 = 73$, $N_2 = 63$, both $P < 0.001$, respectively) and cuckoos received more attacks, than sparrowhawks ($U = 1477.5$, $N_1 = 78$, $N_2 = 73$, $P < 0.001$).
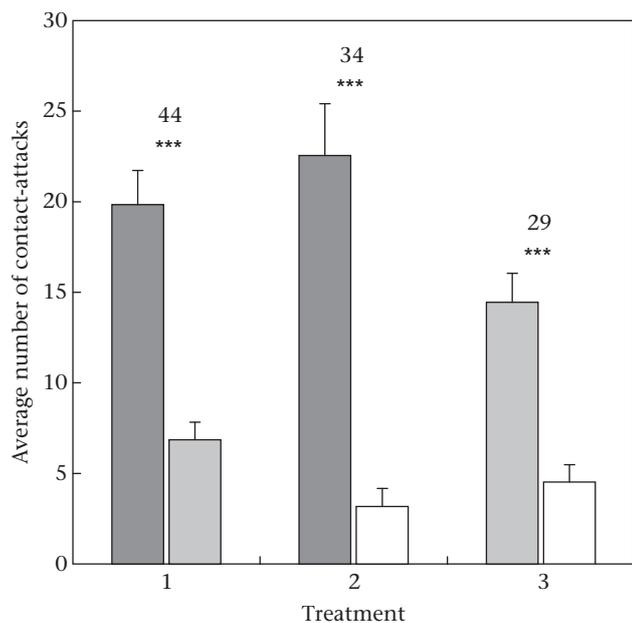
Figure 1. Aggressive responses (average number of attacks + SE) of great reed warblers to the mounts of the cuckoo (dark grey columns), the sparrowhawk (pale grey columns) and the turtle dove (white columns) in three treatments. Numbers at the top of the bars indicate sample size. ***$P < 0.001$.

Table 2
Relative variable importance (i.e. the sum of Akaike weights), model averaged estimates, SE and 95% CI for each term across the two candidate models predicting the number of attacks by great reed warblers

	Relative variable importance	Estimate	SE	Lower CI	Upper CI
(Intercept)		5.58	0.22	5.15	6.00
Mount attacked	1.00	−2.15	0.14	−2.41	−1.88
Stage	1.00	−1.32	0.11	−1.54	−1.10
Treatment	1.00	0.23	0.07	0.09	0.37
Mount attacked*stage	1.00	0.75	0.07	0.62	0.88
Mount attacked*treatment	0.38	0.02	0.04	−0.06	0.10

DISCUSSION

Treatments 2 and 3, in which the mounts of the cuckoo and the sparrowhawk were paired with the mounts of the turtle dove, clearly revealed that great reed warblers discriminate the two enemies from harmless species. Parents always attacked cuckoos and sparrowhawks more frequently than turtle doves, suggesting that they considered both species a danger to their broods. This finding is in accordance with the results from previous studies in which these species were tested separately (Moskát 2005; Požgayová et al. 2009; Honza et al. 2010). More importantly, however, our treatment 1, in which we confronted the tested birds with the simultaneously presented mounts of the cuckoo and the sparrowhawk, revealed that great reed warblers also clearly discriminate between these two species. Parents attacked the mounts of the cuckoo more frequently than sparrowhawk mounts, in all probability because the cuckoo poses less of a threat to them but a larger threat to their current reproductive investment (as a brood parasite or nest predator, Rothstein 1990; Moskát 2005), whereas the sparrowhawk is the biggest threat mainly to

themselves (Cramp & Simmons 1980) as it specializes on hunting adult birds, and only occasionally takes nestlings (Weidinger 2009), but never eggs. Hence, these results also make functional sense (see also Duckworth 1991; Welbergen & Davies 2008).

This behaviour partially differs, however, from that found in other species such as reed warblers, which unlike great reed warblers never or only rarely attacked the mounts of the sparrowhawk (Duckworth 1991; Welbergen & Davies 2008), probably because of their smaller size and greater vulnerability, which may result in their lesser willingness to put themselves at risk (Montgomerie & Weatherhead 1988). In the light of these results, therefore, a question arises: why then do great reed warblers put themselves at risk by attacking the mounts of sparrowhawks? One of the explanations proposed in a previous study also on great reed warbler nest defence (Honza et al. 2010) is that the tested birds might simply mistake separately presented sparrowhawks for cuckoos because of their resemblance. The absence of cuckoo–hawk discrimination is mainly known in birds with no history of cuckoo parasitism (Welbergen & Davies 2008), although possible recognition mistakes are also thought to occur in other suitable cuckoo hosts, such as blackcaps, *Sylvia atricapilla* (Grim 2005a). Finally, Lindholm & Thomas (2000) provided positive evidence that certain hosts (in at least some of their populations) may not even differentiate between the cuckoo and the sparrowhawk. Our results, however, rule out this hypothesis revealing that great reed warblers are selective in their attacks. Instead, a more plausible explanation may be that great reed warblers attacked sparrowhawk mounts because this strategy may be less costly than an enemy-specific nest defence. More specifically, when a parent encounters an unknown intruder near its nest, it must quickly evaluate whether the visitor poses an immediate threat to its nest or itself. Closer inspection of the potential predator to preclude possible predation, however, takes time. Moreover, limited discrimination ability, constricted visibility and time pressure may lead to a higher rate of recognition errors, in particular when the intruder resembles the known enemy. Thus, if there is an immediate danger of nest predation or nest parasitism, as was also simulated in our treatments 2 and 3, more aggressive and bold host species such as great reed warblers may respond aggressively to both nest parasites and predators near their nests regardless of the threats posed by them. This could also partially support the generalized nest defence hypothesis (see also Grim 2005a). Finally, great reed warblers might attack the mounts of the sparrowhawk in order to defend their mates, or simply because they do not consider them dangerous to themselves as they have almost no previous experience with these raptors in their nesting grounds. Although these alternatives seem the least plausible, additional research is necessary to test them.

Nest defence behaviour of great reed warblers in relation to cuckoos and sparrowhawks showed different patterns during the breeding cycle. While cuckoo mounts were attacked more often during the late egg-laying stage, responses to the mounts of

Table 1
Results of Wilcoxon signed-ranks tests comparing aggressive responses of great reed warblers when confronted with three combinations of simultaneously presented dyads of cuckoo, sparrowhawk and turtle dove mounts

	Late egg-laying stage					Late nestling stage				
	Mean	SE	N	Z	P	Mean	SE	N	Z	P
Treatment 1										
Cuckoo	21.61	2.34	23	4.11	<0.001	17.90	3.01	21	2.49	0.013
Hawk	6.30	1.30	23			7.48	1.46	21		
Treatment 2										
Cuckoo	31.89	3.67	18	3.72	<0.001	12.06	2.62	16	2.72	0.007
Dove	1.39	0.68	18			5.19	1.88	16		
Treatment 3										
Hawk	13.71	2.56	14	2.92	0.003	15.13	2.06	15	3.41	<0.001
Dove	3.14	1.12	14			5.80	1.50	15		

sparrowhawks did not change over the nesting cycle. Given that brood parasites pose the greatest threat to their hosts during the egg-laying stage (Briskie & Sealy 1989; Grim 2005a) whereas sparrowhawks are a threat during all the breeding phases, these patterns reflect the actual threats posed by these two species, which is also in accordance with the dynamic risk assessment hypothesis (Kleindorfer et al. 2005). This also suggests that great reed warblers recognize the cuckoo as a special enemy. Our results, however, differ from those of previous studies, which showed a consistently high level of great reed warbler nest defence against the cuckoo over the entire nesting cycle (Moskát 2005). We would assume that these differences might arise from different methodological approaches, as only the categorical variables of nest defence were employed in the previous study.

Finally, we determined that attacks against primary mount targets in our treatments were mainly initiated by females, which may suggest that they also play a key role in cuckoo recognition. Again, this finding partly differs from that in the previous study on great reed warbler nest defence (Požgayová et al. 2009), which reported that cuckoos were attacked in almost all cases simultaneously by both mates, or by one shortly after the other. However, Požgayová et al. (2009) did not focus specifically on the first attack initiation. Therefore, further experiments should be designed to test this assumption. Similarly, our observations of conspecifics cooperatively attacking the cuckoo mounts may partially support the findings reported by Welbergen & Davies (2008, 2009) and Campobello & Sealy (2010), who observed reed warblers from neighbouring territories approaching the focal nest and even attacking the mount. In the case of the great reed warbler, however, most 'helpers' were probably nonbreeding individuals because we did not find their nests. Future studies are therefore needed to elucidate the possible role of unmated great reed warblers in cooperative nest defence.

In conclusion, our results suggest that if the common cuckoo has evolved the visual mimicry of a sparrowhawk in order to avoid host attacks, this mimicry is unsuccessful not only because it is imperfect and hosts can learn discrimination but also because of the generalized nest defence of more aggressive hosts. Moreover, the results of our treatments with separately and simultaneously exposed mounts of cuckoos and sparrowhawks led to completely different interpretations. The fact that great reed warblers attacked both types of mounts may indicate that they do not discriminate between them. When parents were confronted, however, with the simultaneously presented mounts of these species, they exhibited fine cuckoo–hawk discrimination ability. Thus, although the situations in which the birds have to discriminate at one time between two potential dangerous intruders near their nests are less realistic, our findings point out the importance of choosing the right experimental method in enemy recognition studies, in particular when the tested birds are aggressive and the stimuli are similar (see also Grim 2005a).

Acknowledgments

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