

# Cuckoo–hawk mimicry? An experimental test

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The similarity between many Old World parasitic cuckoos (Cuculinae) and *Accipiter* hawks, in size, shape and plumage, has been noted since ancient times. In particular, hawk-like underpart barring is more prevalent in parasitic than in non-parasitic cuckoos. Cuckoo–hawk resemblance may reflect convergent evolution of cryptic plumage that reduces detection by hosts and prey, or evolved mimicry of hawks by parasitic cuckoos, either for protection against hawk attacks or to facilitate brood parasitism by influencing host behaviour. Here, we provide the first evidence that some small birds respond to common cuckoos *Cuculus canorus* as if they were sparrowhawks *Accipiter nisus*. Great tits and blue tits were equally alarmed and reduced attendance at feeders during and after the presentation of mounted specimens of common cuckoos and sparrowhawks, but not in response to control presentations of collared doves or teal. Plumage manipulations revealed that the strong alarm response to cuckoos depended on their resemblance to hawks; cuckoos with barred underparts were treated like hawks, while those with unbarred underparts were treated like doves. However, barring was not the only feature inducing alarm because tits showed similarly strong alarm to barred and unbarred hawks, and little alarm to barred doves. These responses of tits, unsuitable as hosts and hence with no history of cuckoo parasitism, suggest that naive small birds can mistake cuckoos for hawks. Thus, any cuckoo–hawk discrimination by host species is likely to be an evolved response to brood parasitism.

**Keywords:** brood parasitism; coevolution; cuckoo; mimicry; sparrowhawk

## 1. INTRODUCTION

To human observers, many parasitic cuckoos of the Old World (Cuculinae) look remarkably similar to birds of prey, particularly *Accipiter* hawks (Wallace 1889). They share a close resemblance in size and shape (an elongated body, with long wings and a long tail), in plumage (greyish or brownish upperparts, with paler barred underparts) and in their swift direct flight. Their similarity gave rise to an ancient belief that the disappearance of cuckoos from Europe during the winter months came about because they transformed themselves into hawks (Pliny, in Rackham 1997), a possibility dismissed by Aristotle, who pointed out that cuckoos lack both talons and a hooked bill (Turner 1544). Nevertheless, the resemblance is sufficiently close to often cause confusion; during Edgar Chance's pioneering studies of the common cuckoo *Cuculus canorus*, the female that he followed for five successive seasons was mistaken by a local villager for a sparrowhawk *Accipiter nisus* and was about to be shot, when Chance interrupted just in time (Chance 1940).

Hawk-like plumage, with cryptic upperparts and pale barred underparts, is more prevalent in parasitic than in non-parasitic cuckoos (Payne 1967), and most probably evolved after the evolution of brood parasitism, which suggests that these characteristics somehow aid the success of parasitic laying (Krüger *et al.* 2007). Hawks and cuckoos are not closely related, so there are two possibilities for how the resemblance to *Accipiter* hawks might have evolved.

- (i) *Convergent evolution.* Hawks and parasitic cuckoos may have independently evolved similar cryptic plumage to reduce the chances of detection by their victims, respectively, prey and hosts. Crypsis is enhanced by countershading, with a darker dorsal surface and paler underparts, and barring of the underparts may help to break up the body outline while perched among twigs and branches (Newton 1986). Flight behaviour may also be convergent. Sparrowhawks make a series of rapid flaps alternating with glides. During a surprise attack on a prey, the final approach is usually made on a glide, which makes the approaching hawk harder to detect (Newton 1986). Female common cuckoos likewise glide down from their lookout perch to the host nest during their rapid, secretive laying visit (Chance 1940).
- (ii) *Evolved mimicry of hawks by parasitic cuckoos.* Wallace (1889) suggested that the resemblance was an example of protective mimicry, which might reduce attacks from hawks, noting that cuckoos were otherwise 'an exceedingly weak and defenceless group of birds'. Prolonged periods of surveillance for host nests, sometimes from exposed perches, might make parasitic cuckoos especially vulnerable to hawk attack. In Asia, drongo-cuckoos (*Surniculus lugubris*) may likewise gain from protective mimicry of drongos *Dicrurus* spp., which are extremely aggressive to larger birds, including birds of prey and crows (Wallace 1889; Duckworth 1997). Alternatively, hawk mimicry might influence host behaviour, either by frightening or luring hosts away to facilitate egg laying or by inducing mobbing to help the cuckoo locate host nests, which may be especially advantageous in open country with few secret vantage points (Craib 1994).

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Although there is a cuckoo-hawk resemblance from a human perspective, and there are plausible hypotheses for its evolution, the key question remains: do potential receivers in nature regard parasitic cuckoos as hawk-like? Here, we focus on the responses of small birds vulnerable to *Accipiter* hawk attack. Previous experiments have shown that host species exploited by the common cuckoo are more likely to attack a mount of a stuffed cuckoo near their nest than are species that are not vulnerable to cuckoo parasitism, owing to inaccessible nests or an unsuitable diet for raising young cuckoos (Moksnes *et al.* 1991; Røskoft *et al.* 2002). However, without comparative data on their responses to hawks, we cannot conclude that hosts have evolved the ability to recognize the cuckoo as a specific enemy; they may simply be prepared to take more risks in nest defence because their nest is vulnerable to brood parasitism. Only one host species has been tested with both common cuckoo and sparrowhawk mounts near the nest. Reed warblers (*Acrocephalus scirpaceus*) often mob and sometimes attack a stuffed cuckoo, whereas they are much more wary of a stuffed sparrowhawk (Duckworth 1991; Welbergen & Davies *in press*). This certainly shows that reed warblers distinguish cuckoos from hawks, but again we cannot conclude that this is an evolved response to brood parasitism; perhaps non-hosts have this ability too. We suggest, therefore, that it should first be tested whether naive small birds, which have no history of cuckoo parasitism, regard parasitic cuckoos as hawk-like.

Our experiments involve great tits (*Parus major*) and blue tits (*Parus caeruleus*), unsuitable as hosts because they nest in small tree holes that are inaccessible to laying female common cuckoos. They feed in woodlands and hedgerows, where they are vulnerable to attack from sparrowhawks, and form a major component of the sparrowhawk's diet throughout the year (Newton 1986). Furthermore, tits vary their feeding behaviour in response to the risk of sparrowhawk attacks (Hinsley *et al.* 1995; Gosler *et al.* 1995; Gentle & Gosler 2001), and so they are an ideal model to test the effectiveness of cuckoo-hawk resemblance.

We performed two experiments using taxidermic mounted specimens presented at feeders. In the first experiment, we compared tit alarm responses to sparrowhawks (the dangerous enemy) and common cuckoos (the putative mimic, of no threat to adult survival in small birds). In the second experiment, we tested whether alarm responses to cuckoos varied with cuckoo-hawk resemblance by manipulating underpart barring (prevalent in parasitic cuckoos).

## 2. MATERIAL AND METHODS

### (a) Study sites

Observations were made at several peanut feeders set up at three sites: Cambridge (UK), including the University Botanic Garden (1.5 km south of the city centre); Madingley Wood (5 km to the west of Cambridge city centre); and Wicken Fen (15 km northeast of Cambridge city centre). All three sites have nest-boxes with dense breeding populations of both blue tits and great tits. The distances between the sites were as follows: Cambridge to Madingley Wood, 6 km; Cambridge to Wicken Fen, 17 km; and Madingley Wood to Wicken Fen, 19 km. The first experiment was performed from November 2006 to March 2007 and the second from

November 2007 to February 2008. Sparrowhawks were seen daily at all three study sites. Common cuckoos are summer visitors to Britain (April–July) and so were absent throughout the study period. In summer, they breed on Wicken Fen but are rarely seen in Cambridge or Madingley Wood (no recent breeding records).

The feeders were wire mesh tubes (30 cm long and 7 cm in diameter) surrounded by a wire cage (maximum diameter 19 cm), which allowed access by small birds but kept corvids and squirrels at bay. The feeders were suspended from trees, 2 m above the ground. For the first experiment, there were 11 feeders: four in Cambridge; two in Madingley Wood; and five on Wicken Fen. For the second experiment, there were 12 feeders: the same four plus two new feeders in Cambridge; the same two in Madingley Wood; and four of the five on Wicken Fen. The neighbouring feeders within a site were 300 m–1.7 km apart. Observations of colour-ringed individuals (28 blue tits and 27 great tits in the first winter; 19 blue tits and 21 great tits in the second) showed that most individuals fed at only one feeder (91% in the first winter and 92% in the second). Therefore, within each winter, feeders can be regarded as independent samples.

At all feeders, the vast majority of feeding visits were by great tits and blue tits, with a maximum per feeder of 4–22 individuals within 3 m at any one time. There were occasional visits by greenfinches (*Carduelis chloris*), coal tits (*Parus ater*), long-tailed tits (*Aegithalos caudatus*), marsh tits (*Parus palustris*) and nuthatches (*Sitta europea*). However, during the total 138 hours observations (6 hours per feeder per experiment), only 5% of minutes had a visit by one of these other species, and of these most (89%) also included a visit by a great or blue tit. Therefore, although visits by all species were recorded, the responses we analysed were largely the result of the behaviour of great and blue tits.

### (b) Mounted specimens

We recorded the responses of feeding birds to taxidermic mounts of four species, all of similar body length: male sparrowhawk (29–34 cm); common cuckoo (32–36 cm); collared dove (*Streptopelia decaocto*; 31–34 cm); and teal (*Anas crecca*; 34–38 cm). The collared dove was resident at all three sites and was chosen as a familiar harmless control, rather similar to the cuckoo in shape. The teal, a small duck, was chosen as a second harmless control for novelty (teal do not appear at tit feeders!). Two stuffed mounts were used for each species: an adult male sparrowhawk (blue-grey upperparts and pale barred underparts with a rufous tinge) and a juvenile male sparrowhawk (brownish upperparts, pale barred underparts); two adult cuckoos (blue-grey upperparts, pale barred underparts); two collared doves (pale buff-grey, with plain underparts); and a male teal (grey body and red and green head) and a female teal (all brown). The sparrowhawk and teal specimens were chosen to represent the extremes in plumage of these two species. Each mount was placed on a wooden perch and set in a natural posture for the species: an upright stance for the sparrowhawks; body axis slightly raised for cuckoos and collared doves; and horizontal for teal. To protect the specimens from damage, each was housed in a small cage (20×20×30 cm) made from thin black chicken wire (mesh 1 cm<sup>2</sup>) through which the specimens were clearly visible. In a parallel study (Welbergen & Davies *in press*), the responses of reed warblers to these caged cuckoos (intense mobbing) and caged sparrowhawks

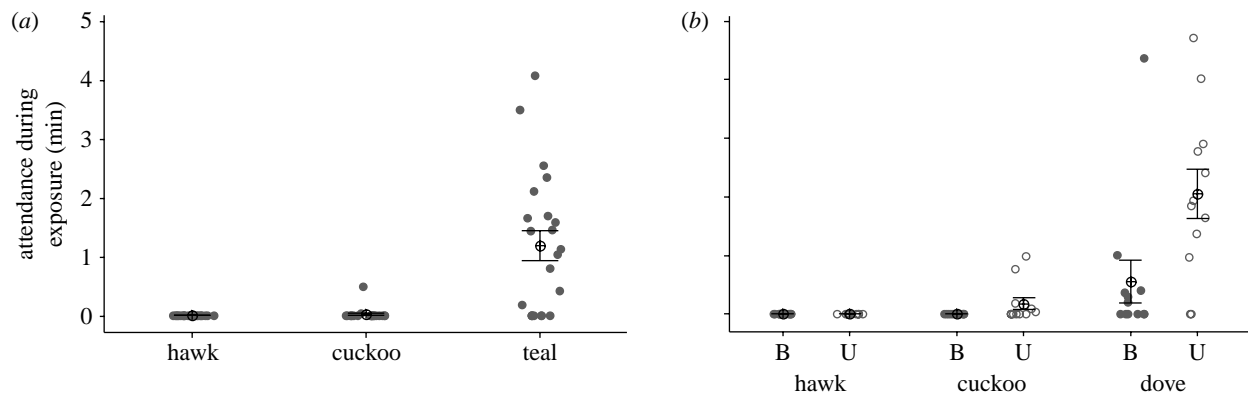


Figure 1. Time birds spent on the feeder during 5 min exposure to mounts placed 50 cm away. Data shown for each feeder, together with means ( $\pm 1$  s.e.) for responses to each mount type. (a) Experiment 1 ( $n=11$  feeders), comparing feeder attendance during exposure to sparrowhawks, common cuckoos and teal. (b) Experiment 2 ( $n=12$  feeders), comparing feeder attendance during exposure to sparrowhawks, common cuckoos and collared doves, each with either barred (B) or unbarred (U) underparts.

(avoidance) were similar to those to uncaged specimens in Duckworth's (1991) study.

To manipulate the underpart barring of the sparrowhawk, cuckoo and dove, we cut two identical pieces of white silk for each specimen. These could be pinned to the underparts, stretching from the upper breast to where the legs met the belly, and up the flanks to the line of the wings on either side. One piece, used for the 'unbarred' treatment, was plain white and obscured the natural barring of the sparrowhawk and the cuckoo. The other, for the 'barred' treatment, had black bars made with a felt-tip pen, of the same width (1–2 mm) and spacing (5 mm) as those on sparrowhawks and cuckoos.

### (c) Experimental protocol

Each trial began with the observer approaching the feeder (at which point any birds left) and standing directly below it for 1 min. The observer then retreated to a recording position 20 m away. (This same recording position was used for all subsequent stages of the trials.) Then began a 30 min period of pre-exposure observation during which all arrivals at and departures from the feeder were noted. This enabled us to score for each minute the number of seconds for which there was one or more birds on the feeder, which we used as our measure of baseline feeder attendance.

Subsequently, there followed a 5 min period of exposure to a mounted specimen, placed 50 cm from the feeder and at the same height. The exposure period began when the first bird approached to within 3 m of the feeder and any arrivals at the feeder and departures were again noted. There was no significant variation across mount specimens in time to first approach within 3 m (Friedman tests: experiment 1,  $S_5=6.01$ ,  $p=0.31$ ; experiment 2,  $S_5=3.10$ ,  $p=0.68$ ). Therefore, tits had similar exposure to all mount specimens. After 5 min exposure, the specimen was removed (with the observer once more standing directly below the feeder for 1 min), and there was another 30 min post-exposure observation period. In both the experiments, a feeder had just one trial per day, with 1–6 days between successive trials.

In the first experiment, each feeder experienced a hawk, cuckoo and teal in sequence (following a Latin-square design). We decided on which of the two specimens for each by the toss of a coin. Then, the three mount types were presented in sequence again (following a new Latin-square design), this time using the other specimen. Therefore, each of the 11 feeders experienced all six specimens.

In the second experiment, each feeder experienced a hawk, cuckoo and collared dove in sequence (following a Latin-square design). We decided on which of the two specimens for each by the toss of a coin, and on which treatment (barred or unbarred) by another coin toss. Then, the three mount types were presented again (following a new Latin-square design), using the same specimens but now with the alternative barred/unbarred treatment. Therefore, each of the 12 feeders experienced six trials.

### (d) Statistical analysis

We used MINITAB for Windows (v. 14.0, Minitab, Inc.). Data were assessed for normality and constant error terms, and transformed if necessary. If transformation was not possible, then the data were dichotomized or non-parametric tests were used. All tests were two-tailed. Feeder attendance was measured as the time during a trial that there were one or more birds on the feeder. We analysed two effects of the mounts. (i) Feeder attendance during the 5 min exposure to the mount. Here, we used a binary logistic regression, scoring trials simply as having some versus no attendance. (ii) Feeder attendance during the 30 min after exposure minus the 30 min before exposure. These data were analysed using general linear models. Models in both (i) and (ii) included three fixed factors: mount species; specimen (nested within mount species); and study site (Cambridge and Madingley Wood, where there are no breeding cuckoos, versus Wicken Fen, where cuckoos breed). Feeder (nested within site) was entered as a random factor and trial order as a covariate.

## 3. RESULTS

### (a) Experiment 1: comparing responses to sparrowhawks and cuckoos

Comparing feeder attendance versus no attendance while the mount was next to the feeder, a binary logistic regression model (log likelihood =  $-12.07$ ,  $G_{16}=56.83$ ,  $p<0.001$ ; goodness of fit: Pearson  $p>0.97$ ) revealed a clear effect of mount species (figure 1a). Attendance was more likely during exposure to teal than to cuckoos ( $Z=2.56$ ,  $p<0.001$ ) or to hawks ( $Z=2.59$ ,  $p<0.001$ ), but there was no difference between cuckoos and hawks ( $Z=0.03$ ,  $p=0.98$ ). There were no effects of feeder ( $Z<1.62$ ,  $p>0.11$ ), study site ( $Z=0.01$ ,  $p=0.99$ ), specimen ( $Z<0.80$ ,  $p>0.43$ ) or trial order ( $Z=0.29$ ,  $p=0.77$ ).

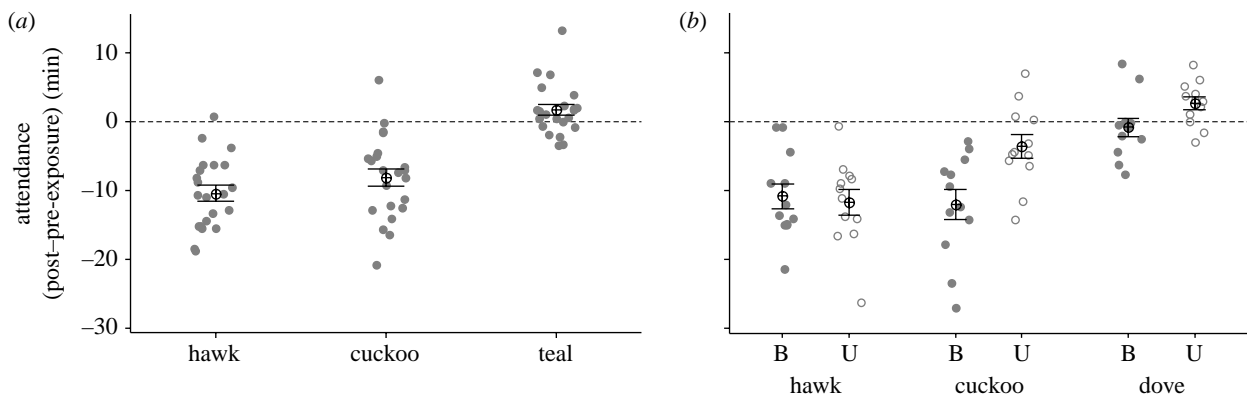


Figure 2. Time birds spent on the feeder during 30 min periods of post-exposure minus pre-exposure to the mounts (therefore, negative values indicate reduced attendance post-exposure). Data shown for each feeder, together with means ( $\pm 1$  s.e.) for responses to each mount type. (a) Experiment 1 ( $n=11$  feeders), comparing responses to sparrowhawks, common cuckoos and teal. (b) Experiment 2 ( $n=12$  feeders), comparing responses to sparrowhawks, common cuckoos and collared doves, each with either barred (B) or unbarred (U) underparts.

During both the hawk and cuckoo presentations, blue and great tits were obviously alarmed; they tended to retreat and remain well above the mounts, usually 2–10 m away (small birds are more vulnerable to hawk attacks from above), erected their head feathers and often turned rapidly from side to side while perched, giving ‘chicka’ alarm calls. By contrast, they often visited the feeders during teal presentations and sometimes fed with their back to the mount, apparently unconcerned by its presence.

To analyse the effect of the mounts on subsequent feeder attendance, we calculated attendance during the 30 min after exposure minus that during the 30 min before exposure (figure 2a). A general linear model showed that this change in feeder attendance varied significantly with mount species presented ( $F_{2,48}=37.85$ ,  $p<0.001$ ). After exposure to teal, the tits quickly settled down to baseline levels of feeder attendance, whereas after cuckoo or hawk exposure they were reluctant to visit the feeder and often left after short visits. As a result, attendance after both cuckoo and hawk exposure was reduced significantly compared with that after teal exposure (Tukey–Kramer tests,  $t=6.67$ ,  $p<0.001$  and  $t=8.21$ ,  $p<0.001$ , respectively), with no significant difference between the effects of cuckoos and hawks ( $t=1.58$ ,  $p=0.21$ ). There was no effect of feeder ( $F_{9,48}=1.70$ ,  $p=0.12$ ), study site ( $F_{1,48}=2.83$ ,  $p=0.13$ ), mount specimen ( $F_{3,48}=1.08$ ,  $p=0.37$ ) or trial order ( $F_{1,48}=0.32$ ,  $p=0.58$ ). The latter is an important result; it indicates that time between trials was sufficient for birds to have settled down to the normal baseline activity before the next presentation. Furthermore, there was no effect of time to first approach during the exposure phase ( $F_{1,48}=0.97$ ,  $p=0.33$ ), so the results were not confounded by any variation in exposure birds had to the mounts.

#### (b) Experiment 2: influence of underpart barring on responses

Comparing feeder attendance versus no attendance while the mount was next to the feeder, a binary logistic regression model (log likelihood =  $-14.66$ ,  $G_{17}=59.30$ ,  $p<0.001$ ; goodness of fit, Pearson  $p>0.96$ ) revealed a significant effect of mount species (figure 1b). Feeder attendance was more likely during exposure to collared doves than to cuckoos ( $Z=2.38$ ,  $p<0.017$ ) or to hawks ( $Z=2.41$ ,  $p<0.016$ ), but there was no difference between

cuckoos and hawks ( $Z=0.03$ ,  $p=0.97$ ). There was also a significant effect of barring, with attendance more likely during the presentation of unbarred mounts than barred mounts ( $Z=2.00$ ,  $p=0.045$ ). There was no significant interaction between mount species and barring ( $Z=0.05$ ,  $p>0.96$ ) and no effects of feeder ( $Z<1.74$ ,  $p>0.08$ ), study site ( $Z=1.07$ ,  $p>0.28$ ) or trial order ( $Z=0.52$ ,  $p=0.60$ ).

Extending this analysis beyond the scores of simply attendance versus no attendance, we considered the time spent on the feeder during mount exposure (figure 1b). Within the 12 feeders, there was significant variation in time spent on the feeder during exposure to the six mount types (Friedman test:  $S_5=37.94$ ,  $p<0.001$ ). There was no attendance during exposure to either barred or unbarred hawks. However, attendance was higher during the presentation of unbarred specimens for both cuckoos and doves (Bonferroni-corrected Wilcoxon signed-rank tests: exact  $p=0.093$  for barred versus unbarred cuckoos and exact  $p=0.006$  for barred versus unbarred doves).

Considering now the change in feeder attendance after mount exposure (attendance during the 30 min post-minus pre-exposure periods; figure 2b), a general linear model showed a significant effect of mount species ( $F_{2,50}=36.63$ ,  $p<0.001$ ), barring ( $F_{1,50}=9.47$ ,  $p=0.003$ ) and an interaction between the two ( $F_{2,50}=4.23$ ,  $p=0.02$ ). For hawks, there was no difference in tit response to barred and unbarred specimens; both caused a marked reduction in feeder attendance (Tukey–Kramer test:  $t=0.05$ ,  $p=1.00$ ). Likewise, there was no significant difference in tit response to barred and unbarred doves ( $t=1.35$ ,  $p=0.76$ ). Therefore, although tits had been more reluctant to feed during exposure to barred than unbarred doves (figure 1b), they quickly settled back to pre-exposure feeding attendance after presentations of either specimen (figure 2b). However, barring had a marked effect on tit responses to cuckoos ( $t=4.00$ ,  $p=0.003$ ; figure 2b). The tits treated barred cuckoos like hawks (compared with barred hawks  $t=0.28$ ,  $p=0.99$  and with unbarred hawks  $t=0.23$ ,  $p=0.99$ ) and unbarred cuckoos more like doves (compared with barred doves  $t=1.35$ ,  $p=0.76$  and with unbarred doves  $t=2.76$ ,  $p=0.08$ ; compared with barred hawks  $t=3.57$ ,  $p=0.01$  and with unbarred hawks  $t=3.79$ ,  $p=0.005$ ). There was no effect of feeder ( $F_{10,50}=1.35$ ,  $p=0.23$ ), study

site ( $F_{1,50}=2.90$ ,  $p=0.12$ ) or order of presentation ( $F_{1,50}=0.49$ ,  $p=0.49$ ). Furthermore, there was no effect of time to first approach to the mount during the exposure phase ( $F_{1,50}=1.21$ ,  $p=0.28$ ), so the results were not confounded by any variation in exposure to the mounts.

We compared tit responses in the two experiments (figure 2a,b), controlling for feeder identity in a GLM. There were no differences in the effects of the two controls, teal and unbarred collared doves ( $F_{1,18}=0.07$ ,  $p=0.79$ ), nor between natural sparrowhawk specimens and those with the barred silk treatment ( $F_{1,18}=0.00$ ,  $p=0.97$ ), nor between natural cuckoos and those with the barred silk treatment ( $F_{1,18}=2.15$ ,  $p=0.16$ ).

#### 4. DISCUSSION

We found clear differences in tit responses depending on the mounted species to which they were exposed. During the presentations of the two harmless controls, a familiar collared dove and a novel teal, the tits often continued to visit the feeders and afterwards their attendance returned to pre-exposure levels. By contrast, they avoided the feeders during and after both sparrowhawk and cuckoo presentations. The most striking result from experiment 1 was that the response was similar to sparrowhawks and cuckoos, even though cuckoos are of no threat to adult tits.

The plumage manipulations in experiment 2 suggested that the strong alarm response to cuckoos depended on their resemblance to hawks, because when their hawk-like underpart barring was obscured, the tits treated them as no more of a threat than doves. This supports the idea that the evolution of barring in parasitic cuckoos, revealed by the comparative analysis (Payne 1967; Krüger *et al.* 2007), enhances their resemblance to hawks. However, underpart barring cannot be the only feature inducing an alarm response because the tits showed equally strong alarm to barred and unbarred hawks. Furthermore, little alarm was shown to barred doves. Therefore, the underpart barring must combine with other cuckoo features, for example their grey upperparts and elongated wings and tail, to cause hawk resemblance.

We found no significant effect of specimen, which suggests that these results cannot be attributed to any peculiarities of the particular mounts we used. We also found no effect of study site, so the tits on Wicken Fen, which would have experienced daily encounters with cuckoos during the previous summer, had equally strong responses to cuckoos as the tits in Cambridge and Madingley Wood, which were unlikely to have encountered cuckoos. This suggests that the strong effect of the cuckoo at both sites was not simply one of alarm to a novel stimulus.

Tits attending rich food sources are especially vulnerable to attack, because sparrowhawks learn that these are good locations for finding prey (Hinsley *et al.* 1995). Because sparrowhawks make surprise attacks (Newton 1986; Cresswell 1996), alarm to any hawk-like stimuli is likely to be adaptive, despite the loss of feeding time from frequent false alarms. Nevertheless, the 5 min exposure of the specimens gave the tits ample opportunity for close inspection, so it is remarkable that a cuckoo caused a strong alarm response, given that it lacks a hawk's lethal weapons, namely talons and a hooked beak. If the inspection of a potential dangerous predator is costly,

then even a slight resemblance through shape, grey upperparts and underpart barring may be sufficient to deter approach. Other studies have shown that mimics do not have to resemble the model perfectly to gain protection, especially when signal receivers regard the model as highly noxious or dangerous, or if the model is relatively common (Ruxton *et al.* 2004). Perhaps the tits' response depends not only on the stimulus but also on the context; cuckoos are absent in winter so hawk-like stimuli at this time are more likely to be hawks. Motivation of the signal receiver (value of the resource it is exploiting) may also influence responses to models and potential mimics (Barnett *et al.* 2007; Cheney & Côté 2007). For example, it may pay a more hungry tit to risk a closer inspection of hawk-like stimuli when there is the potential for the stimulus to be a harmless mimic.

Previous work on egg discrimination has shown that both great and blue tits, like other species with no history of cuckoo parasitism, will accept eggs unlike their own. This suggests that the egg rejection exhibited by cuckoo hosts has evolved specifically in response to cuckoo parasitism (Davies & Brooke 1989; Moksnes *et al.* 1991). Our results here show that, at least in one context, great and blue tits respond to adult cuckoos as if they were hawks. This raises the possibility that the discrimination by cuckoo hosts of the adult cuckoo as an enemy distinct from hawks, which can be attacked (Moksnes *et al.* 1991; Duckworth 1991; Welbergen & Davies *in press*), is also an evolved response to cuckoo parasitism. Experiments have revealed that in response to brood parasitism, hosts pay closer attention to the features of their own eggs so they are better able to discriminate foreign eggs (Rothstein 1982; Lotem *et al.* 1995). Similarly, hosts may pay closer attention to multiple features of hawks so they can better discriminate cuckoos. Further studies are now needed to test the features used by cuckoo hosts to distinguish cuckoos from hawks, and to test whether, despite some host discrimination, parasitic cuckoos still gain from hawk resemblance. Just as host improvements in egg discrimination have selected for better cuckoo egg mimicry (Brooke & Davies 1988), so perhaps have improvements in their plumage discrimination selected for better cuckoo-hawk mimicry.

The study followed the guidelines for the treatment of animals in behavioural research and teaching (Association for the Study of Animal Behaviour). The mounted specimens were obtained from licensed taxidermists.

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