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Animal behaviour

Salient eyes deter conspecific nest intruders in wild jackdaws (*Corvus monedula*)

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Animals often respond fearfully when encountering eyes or eye-like shapes. Although gaze aversion has been documented in mammals when avoiding group-member conflict, the importance of eye coloration during interactions between conspecifics has yet to be examined in non-primate species. Jackdaws (*Corvus monedula*) have near-white irides, which are conspicuous against their dark feathers and visible when seen from outside the cavities where they nest. Because jackdaws compete for nest sites, their conspicuous eyes may act as a warning signal to indicate that a nest is occupied and deter intrusions by conspecifics. We tested whether jackdaws' pale irides serve as a deterrent to prospecting conspecifics by comparing prospectors' behaviour towards nest-boxes displaying images with bright eyes (BEs) only, a jackdaw face with natural BEs, or a jackdaw face with dark eyes. The jackdaw face with BEs was most effective in deterring birds from making contact with nest-boxes, whereas both BE conditions reduced the amount of time jackdaws spent in proximity to the image. We suggest BEs in jackdaws may function to prevent conspecific competitors from approaching occupied nest sites.

1. Introduction

Eyes or eye-like stimuli have been shown to elicit vigilant or fearful responses in many animals. For example, basking black iguanas (*Ctenosaura similis*) [1] and jewel fish (*Hemichromis bimaculatus*) [2] respond to eye shapes by fleeing rapidly. Birds, including house sparrows (*Passer domesticus*) [3], starlings (*Sturnus vulgaris*) [4] and jackdaws (*Corvus monedula*) [5], also exhibit fearful responses when presented with heterospecific eyes. These responses have been attributed to an instinctive tendency to avoid stimuli that resemble predator eyes [3]. Although eye avoidance has been most heavily studied in a predator–prey context, there is some evidence to suggest that eyes may also play a role during conflict between conspecifics.

For some animals, direct eye contact can be considered a threatening display. Individuals may avert their gaze (e.g. bonnet macaques (*Macaca radiata*) [6]) or move away (e.g. Eurasian jays (*Garrulus glandarius*) [7]) to avoid incurring aggressive responses. Primates have been postulated to benefit from having round, dark-coloured eyes, because these features conceal their gaze direction [8]. This is in contrast to the oval-shaped human eye which exposes the white sclera surrounding the coloured iris. These features may have evolved to facilitate communication, promote cooperative social engagement and discourage anti-social behaviour through detectable eye gaze [8,9]. The role of eye salience in interactions between conspecifics outside of the primate lineage remains unexplored. Here, we investigate whether brightly coloured eyes serve as a deterrent to intruders in wild jackdaws during nest exploration.

Jackdaws are colonial breeders and one of the few corvid species that nest in cavities. Cavities are typically a limiting resource, so competition for nest sites is intense, and jackdaws occasionally approach or enter nest sites which are

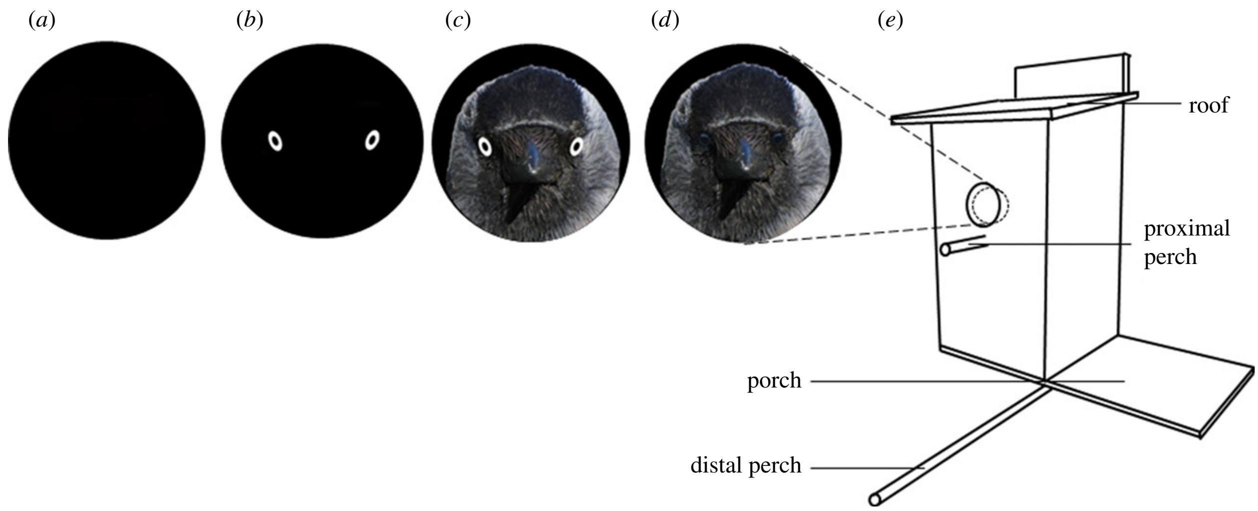

Figure 1. Four stimulus types: (*a*) control (C); (*b*) eyes only (EO); (*c*) bright eyes (BE) and (*d*) dark eyes (DE) placed inside the nest-box (*e*). (Online version in colour.)

not their own [10,11]. Unlike most of their corvid relatives, jackdaws have near-white irides, which are conspicuous against their dark feathers. The salience of the eyes can be seen when jackdaws are inside their nest, often visible when viewing from the outside (G.L.D. 2011, personal observation). We suggest that jackdaw eyes may act as a warning signal to indicate that a nest is occupied and deter other jackdaws from approaching. To test this, we conducted an experiment where we attached images inside nest-boxes such that they were visible to prospector jackdaws from the outside. We designed four different stimulus types: a jackdaw head with natural BEs and a jackdaw head with dark eyes (DEs) were used to test the effect of eye coloration. Isolated BEs only were used to test whether eyes alone elicit a prey-like fear response in jackdaws, and a black circle was used as a control to ensure that the jackdaws were not responding to an unfamiliar object or nest disturbance by the experimenter. If jackdaws' BEs are effective deterrents against conspecific competitors, then we predicted that jackdaws prospecting potential nest sites should be least likely to approach and spend less time close to nest-boxes displaying a jackdaw image with BEs.

2. Material and methods

Four circular images approximating the size of a jackdaw head (6.3 cm diameter) were created using Adobe Photoshop (figure 1). The control image (C) was a solid black circle. The jackdaw with BE image was a face-on photograph of a jackdaw. We adjusted the eyes so they were symmetrical and solid white owing to the photograph showing some shading artefacts on the iris. The jackdaw with DEs image used superimposed DEs isolated from a photograph of a rook (*Corvus frugilegus*), a sympatric corvid species. The eyes-only (EO) image was composed of the eyes isolated from the BE image. All images were laser printed to Zecom WeatherWriter waterproof paper.

Eighty nest-boxes located over 14 distinct areas in Madingley, Cambridgeshire were randomly allocated one of the four treatment types during the pre-breeding season (February–April 2013) when jackdaws prospect for potential nest sites. The image was suspended inside the box, 5 cm behind the entrance hole (8 cm diameter) using garden wire fixed to the underside of the roof. A camouflaged video camera and tripod filmed the area surrounding the box from the ground. All boxes were north or northeast facing, and trials occurred between the hours of 06.00 and 09.00 (except one box between 10.00 and 12.00) to control for lighting effects across boxes. Each trial lasted between 120 and 185 min. A maximum of four trials at different boxes were conducted during the same time period, with each box in a distinct nesting area. Of the 80 boxes given treatments, 32 were included in the analysis because they received at least one jackdaw visit to the box or on a nearby branch in front of the box (C = 6, EO = 9, BE = 7, DE = 10).

Videos were analysed using Observer XT software (Noldus Information Technology) to record the duration and number of times a jackdaw visiting a nest-box made contact with the box, at four positions: nest-box roof, side platform, distal perch (protruded 29 cm from nest entrance at bottom corner of nest-box) and proximal perch (protruded 1 cm below nest entrance; figure 1*e*; and see the electronic supplementary material). Videos (28%) were analysed by a second blind coder (Cohen's weighted Kappa; distinct box visits = 0.90, perch duration = 0.96). Boxes were located in woodland areas with tree branches at varying distances from the nest-boxes. To account for any differences in behaviour based on viewing the image from afar, we analysed the number of distinct visits to the box. A visit was considered distinct when a jackdaw that was previously not in contact with the box (such as on a nearby branch or out of frame) made contact with the box. This measure included birds' initial approach from afar and repeated visits following the initial approach. In addition, to determine whether the image types influenced visit durations and proximity to the nest entrance hole, we analysed the time jackdaws spent on the proximal perch out of the total proportion of time on both perches. We used MASS [12] and lme4 [13] packages for R v. 3.0.2 [14] to run generalized linear models fit to a negative binomial distribution with a log link function for the first analysis, and a quasi-binomial distribution for the second analysis, because our data showed overdispersion. Image type was included as a fixed factor, and the control was used as the reference category. Model assumptions were checked, and a likelihood ratio test determined whether variation explained by the model was improved with the inclusion of trial length.

3. Results

Relative to the control condition, jackdaws made contact with the nest-box significantly less often only when BE was displayed ($z = -2.13$, $p = 0.034$). There was no significant effect for DE ($z = -0.258$, $p = 0.80$) or EO ($z = -1.59$, $p = 0.113$; figure 2*a*). Trial length was excluded as it did not

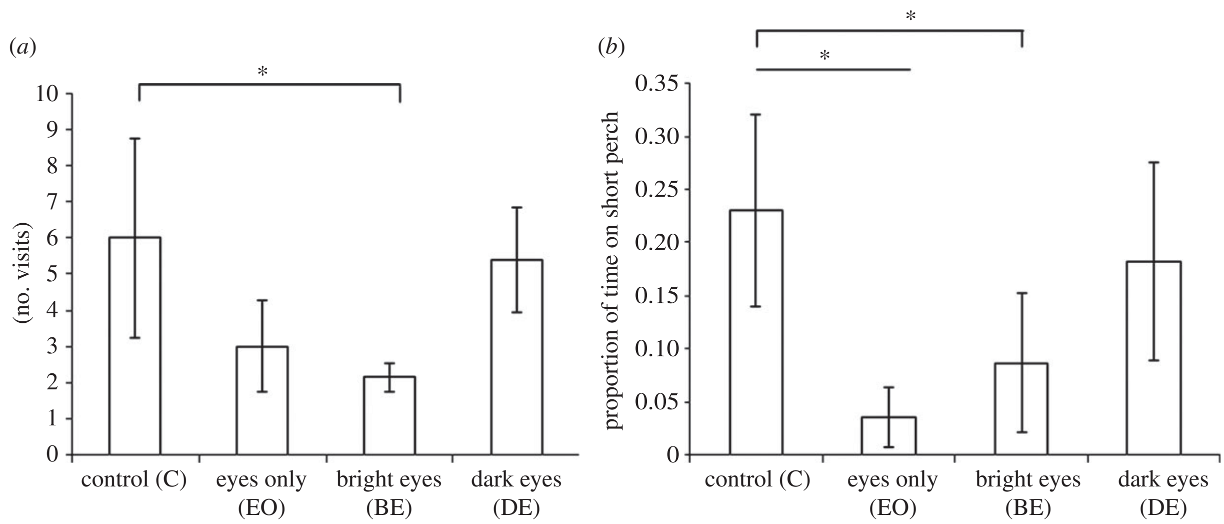

Figure 2. (*a*) Jackdaws visited the nest-box less during the BE condition than in the control; (*b*) out of total time on both perches, jackdaws spent less time on the proximal perch during the EO and the BE conditions (means ± s.e.) $^*p < 0.05$, reference category = control.

improve the model fit ($\chi^2(1) = 3.66$, $p = 0.06$). Analysis of proportion of time (in ms) spent on the proximal perch showed jackdaws spent a significantly lower proportion of time on the short perch relative to the control when the two BE conditions were displayed (EO, $z = -2.075$, $p = 0.048$; BE, $z = -2.307$, $p = 0.029$). The DE condition did not differ from the control ($z = 0.825$, $p = 0.417$; figure 2*b*). There were two instances when jackdaws entered the nest-box, one during the control and one during DE.

4. Discussion

To the best of our knowledge, this is the first demonstration that eye coloration may be important for communication between conspecifics outside of the primate lineage. Jackdaws avoid approaching nest sites, presumably, because eyes may indicate that a nest-box is currently being defended by another jackdaw. Jackdaws also spend less time near the entrance hole when EO is displayed, suggesting that once prospectors have decided to visit a box salient eyes may be sufficient for reducing the time they remain in proximity to the nest entrance. A jackdaw face with DEs was not effective in deterring jackdaws from visiting nest-boxes or approaching entrance holes.

Our results suggest the pale iris may serve as a signal during nest defence. Jackdaws are most likely to prospect at other nest sites if the owners are absent [10], possibly, because attacks by owners can lead to injury or death. Therefore, intense conflict could be avoided if jackdaws inside the nest-box are visible to competitors from the outside, and this may be facilitated by the conspicuousness of the iris. Jackdaws are unique among their *Corvus* relatives as they are both cavity nesters and have pale irides. Whether conspicuous eyes are important for other cavity nesting birds remains to be explored, and could be investigated through phylogenetic comparative methods.

Jackdaws may also respond to eyes inside nest-boxes because they have a predisposition to avoid predator-like eyes or even conspicuous shapes [15]. Our study shows that, relative to the control condition, jackdaws approached the nest-boxes less only when the jackdaw image with BEs was displayed, suggesting the context of the eyes (i.e. on a jackdaw face) is important for whether jackdaws approach the nest-boxes. By contrast, jackdaws spent less time next to the nest hole in both EO and BE conditions which may reflect a predisposition to fear eye shapes. Support for the latter interpretation could be investigated by placing predator-like pale eyes (e.g. hawk) in nest-boxes.

Jackdaws may respond to BE, because salient eyes are important for conspecific recognition. Because the eyes were adjusted using imaging software and printed to paper, they may appear unusual to the jackdaws and their response may be attributed to an oddity, rather than an accurate representation of jackdaw eyes. We cannot be certain whether they are responding to them as such, though responses were strongest to the image that most resembled a jackdaw, and there was no apparent response to the oddity of the rook eyes on a jackdaw face. Jackdaws have been shown to be sensitive to eye gaze direction in humans by delaying their approach to food when an unfamiliar human is looking towards them. Moreover, they are able to use a familiar human's eye positioning as an indication of where hidden food is located [5]. Von Bayern & Emery [5] suggested this attentiveness to human eyes may be attributed to the jackdaw's own brightly coloured eyes, but the role of iris colour in jackdaw behaviour has not been tested previously. We have demonstrated a unique context in which iris colour serves to avoid conflict and improve nest defence, warranting further exploration into the function of salient eyes for signalling in birds.

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Data accessibility. Data can be accessed at http://doi.org/10.5061/dryad.m7j4q.

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