

Evaluation of disruptive camouflage of avian cup-nests

TOM MULDER,^{1*}  CORI J. CAMPBELL²  & GRAEME D. RUXTON¹ 

¹School of Biology, Biomedical Sciences Research Complex, University of St Andrews, St Andrews, UK

²Nuffield Department of Medicine, The Peter Medawar Building for Pathogen Research, University of Oxford, Oxford, OX1 3SY, UK

Parent birds employ various strategies to protect their offspring against nest predators. Two well-researched anti-nest-predation strategies involve visual concealment of the nest by way of parental camouflage and egg camouflage. By contrast, camouflage of nest structures is relatively under-researched, particularly in the case of cup-nests in trees and bushes. We explored how birds camouflage cup-nests in nature. Specifically, we tested Hansell's hypothesis that birds use externally applied pale and white objects such as spider cocoons and lichens to achieve cup-nest camouflage. To test Hansell's hypothesis, three complementary experiments were performed: (1) an *in situ* nest predation experiment; (2) a photo-based visual search experiment; and (3) contrast analyses using PAT-GEOM software in IMAGEJ. White paper and chalk spots were used to mimic white objects used by birds in nature. Whereas predation rates in Experiment 1 were not affected by white spots, location rates in Experiment 2 were lower for natural nests with white spots than without white spots. Experiment 3 demonstrated that white spots significantly increased the contrast between different visual elements of nests. It was concluded that white objects can potentially camouflage nests against some nest predators, and that any improved camouflage was probably achieved via disruptive camouflage.

Keywords: contrast, lichens, PAT-GEOM, spider cocoons.

Nest predation can be a substantial selective pressure experienced by parent birds (Martin 1995), which should select for features that reduce detection rates by nest predators, such as visual camouflage. Visual camouflage of parent birds associated with incubation has been well described in the literature (Montgomerie *et al.* 2001, Nokelainen & Stevens 2016, Troscianko *et al.* 2016, Wilson-Aggarwal *et al.* 2016). For example, Mozambique Nightjar *Caprimulgus fossi* parents that better matched background patterns and contrasts incurred lower clutch mortality rates compared with poorly background-matching parents (Wilson-Aggarwal *et al.* 2016). Similarly, camouflage of avian eggs that are visually exposed to potential nest predators when parent birds are temporarily absent from the nest has also been researched on numerous occasions (Tinbergen *et al.* 1962,

Westmoreland & Kiltie, 1996, Lovell *et al.* 2013, Troscianko *et al.* 2016, Gómez *et al.* 2018).

It has been established that eggs with a light ground colour and dark spots experience significantly less predation in both ground-nesters and tree nesters (Westmoreland & Best 1986, Weidinger 2001, Troscianko *et al.* 2016). Moreover, several ground-nesting bird species including Kentish Plovers *Charadrius alexandrinus* and Japanese Quail *Coturnix japonica* enhance egg crypsis by selecting matching egg-laying substrates (Lovell *et al.* 2013, Gómez *et al.* 2018). Crucially, however, whereas camouflage of eggs and parent birds has been researched relatively extensively (Westmoreland & Kiltie 1996, Lovell *et al.* 2013, Troscianko *et al.* 2016, Wilson-Aggarwal *et al.* 2016, Gómez *et al.* 2018), avian cup-nest camouflage has scarcely been researched. This substantial imbalance in research effort appears unjustified, as cup-nests also potentially provide visual cues that can be exploited by nest predators, and cup-nest

*Corresponding author.

Email: tom.mulder@hotmail.com

appearance should consequently also incur selective pressures for visual camouflage.

Some evidence of visual cup-nest camouflage has been provided by captive Zebra Finches *Taeniopygia guttata* that background-matched the colour of nest-building materials when provided with two colour alternatives in the laboratory (Bailey *et al.* 2015). Although testing unnatural nesting materials against an equally unnatural and uniformly coloured background was appropriate for the authors' goals, it removed the variability of nesting materials and backgrounds available to avian nest-builders in nature (Bailey *et al.* 2015). Examination of avian cup-nest camouflage in nature should be illuminating. To this end, Hansell formulated an interesting hypothesis that pale or white coloured spider cocoons, lichens and man-made materials are added to the exterior of the cup nests of a diversity of birds to achieve disruptive cup-nest camouflage (Hansell 1996). Disruptive camouflage reduces predation by disrupting the silhouette of an animal or inanimate object (in this case a nest), giving the illusion of an unsubstancial object of no interest to potential predators through heightening the contrast between different visual elements of the nest (Nokelainen & Stevens 2016).

We examined avian cup-nest camouflage in nature by testing Hansell's hypothesis in a three-fold approach: (1) an *in situ* nest predation experiment; (2) a photo-based visual search experiment with human subjects; and (3) photo-based analyses of contrast values to identify objectively the type of visual camouflage (if any) at work.

METHODS

Experiment 1: *In situ* nest predation experiment

Twenty-six nests were collected from private and permitted public forest patches. Nests were not collected prior to conclusion of the breeding season. Nests were divided into 'brown' ($n = 16$) and 'green' ($n = 10$) nest types. Brown nests were mostly constructed of mud and grasses and twigs, e.g. Common Blackbird *Turdus merula* nests (Mainwaring *et al.* 2014), and green nests were mainly constructed of green mosses and grasses, e.g. Chaffinch *Fringilla coelebs* nests (Hansell, 1996). By drawing lots, nests were subdivided into pairs of green nests and pairs of brown nests.

Exteriorly adhering pale materials were removed from any nests which naturally presented such objects, to control for potential camouflaging effects. In turn, one nest from each pair was camouflaged artificially (these nests are henceforth referred to as 'treated nests') with white spots ($c. 1.5 \times 1.5$ cm, which we expect to be towards the large-size end of the naturally occurring range: Hansell 1996) of bird-safe and odourless liquid chalk (Klaxo Witkalk Bloedluispreventie En Bestrijding (White chalk for blood louse prevention and control), manufactured by Klaxo). Chalk spots were applied in thick layers with clearly defined edges; application was equally easy for both nest types. Ten spots were applied to each treated brown nest and nine spots to each treated green nest, to account for the slightly larger size of the former. Spots on both nest types were placed in such a way that they were approximately equally spaced apart and did not enter into the cup of the nests. The non-treated counterparts of each nest pair constituted the 'controls'. Controls and treated nests would look identical when viewed from directly above; from all other perspectives, the white materials applied influence the visual appearance (at least from some distances).

Nests were placed in shrubs and trees in forest patch edges and baited with a single Japanese Quail egg. Note that during nest collection, we observed the specific microhabitat characteristics associated with nests and used this information to place our experimental nests in realistic situations. Specifically, nests were collected at various depths in shrubs and trees (deciduous and coniferous) in agricultural pasture boundaries as well as in forests. However, as we were interested in relative predation rates across experimentally placed nests and not in estimating absolute predation rates on natural nests, nest-site selection should not be critical to the integrity of our study. Following placement of the first nest of a nest pair (nest A), the second nest (nest B) was placed in a comparably dense tree or shrub of the same species such that nest B was not visible from nest A, and vice versa. Such placement experimentally controlled for visibility differences caused by contrast and colour variation of the background, thus eliminating the need for colour and contrast measurements at this stage. As a result, nest spacing varied from 5 to 20 m depending on the foliage. Within an experimentation site, nest pairs were spaced substantially further apart than two nests of a single pair. Sites

were spaced approximately *c.* 200 km to *c.* 15 km apart, all located in Drenthe, The Netherlands. The habitat types of the sites comprised deciduous forest patches ranging from *c.* 25 m to *c.* 200 m in diameter, as well as deciduous and coniferous tree and shrub boundaries surrounding agricultural pastures.

Two days after placement and baiting of the nests with Quail eggs, the nests were retrieved. Nests were considered 'predated' when the nest was empty and 'not predated' when the egg was present. The described placement/baiting/retrieval procedure was repeated 182 times over the period of the experiment using pairs consisting of the 26 nests we collected. Thus, nests were re-used but their location shifted each time they were re-baited.

For ethical reasons, all tests were conducted shortly after the conclusion of the bird breeding season, specifically from 22 July to 26 August 2019. During the test period, all trees were still fully covered in foliage similar to during the bird breeding season. Although time of year may have influenced the absolute predation we observed, this should not have influenced the relative predation rates experienced by our different types of experimentally placed nests.

Experiment 2: Photo-based visual search experiment

Although there are obvious advantages to using natural predators in Experiment 1, there is the theoretical possibility that our experimental manipulation made nests aversive to predators as well as having an effect on camouflage; that is, there might possibly have been an effect of post-detection decision-making, as well as any effect on detection. To acknowledge this, we also performed Experiment 2, where humans were charged solely with detection of nests. Six nests were obtained to take photographs of nest pairs within foliage. Externally adhering pale and white objects were removed. Nests were arranged into pairs of three nest types: green ($n = 2$), brown ($n = 2$) and man-made brown decorative nests ($n = 2$). The man-made brown nests were 10 cm in diameter, were cup-shaped and were constructed using brown vine twigs. Nests were purchased from House Sill Nature Craft Holiday Decorations via eBay. See Appendix 1 for an image of the nests as advertised online and a link to the advertisement.

White paper spots (*c.* 1.5 × 1.5 cm) were applied to camouflage one-half of the exterior of each nest, and the other half of the nest constituted the non-treated control. As such, 180° rotation of a nest around the vertical axis could either present the treated or the non-manipulated control side of a nest. Notably, five spots were applied to each brown and man-made brown nest, whereas only four spots were applied to each treated green nest to account for the slightly smaller size of the latter. A nest pair of the same nest type was placed in foliage where one faced outward with the control half and the other faced outward with the treated half. Nests were deliberately placed within the foliage, as opposed to in front of the foliage, in locations/microhabitats comparable to where nests were found during the nest-collection phase. A photograph was taken in which both nests were equally in view, yet reasonably hidden. Both nests were then rotated 180° and another photo was taken, resulting in photo pairs that control for variation in ease of detection arising from minor placement differences. Photo pairs were randomly divided into two photo sets, which were examined by separate subject groups (as such, we controlled for any effects of nest placement). The chronology of photos in the photo sets was kept constant. We generated six green nest picture pairs, six brown nest picture pairs and five man-made brown nest picture pairs, for a total of 17 visual search tasks to be completed by each subject.

To initiate the visual search experiment, human subjects ($n = 94$) visually focused on a black spot on their computer screen, which ensured all visual search trials initiated at the centre of upcoming photos. While focusing on the black spot, subjects clicked for the following photo to appear instantly. Subjects searched the photo and noted down the coordinates of the first nest located, using a superimposed coordinate-grid. The black spot reappeared on the next slide and the process was repeated ($n_{\text{repeats}} = 17$). Nests that were not located by subjects were considered 'missed'. No time limit was imposed upon subjects, but all subjects completed the 17 visual search tasks within 5–10 min. Subjects did not repeat trials on pictures they had previously searched. The examination of photos was performed using computers and monitors of the same make, with photos displayed at full screen.

We believe the results of Experiment 2 to be reliable and resultant from a sufficiently

challenging visual search task because subjects took 5–10 min to complete a task with 17 photos, whereas an insufficiently challenging task would have been completed in a substantially shorter time. Moreover, a low error rate (1.4%, see below) indicated that subjects were appropriately engaged in locating nests, and the visual search task was not too difficult to complete accurately. As 94 human subjects completed 17 visual search tasks, we obtained 1598 data points. Twenty-seven errors occurred (1.4% error rate) where subjects noted coordinates without a nest or were unable to locate any nest. Erroneous data points were excluded from the dataset prior to analysis.

Experiment 3: Contrast analyses using PAT-GEOM software in IMAGEJ

Contrast values of the treated nests, control nests and the surrounding background from all photos of Experiment 3 were quantified. The contrast value is a measure of the patterning and texture of the appearance of the nest from a distance, where high contrast suggests strongly non-uniform bold patterning. Contrast values were measured with the ‘Marking Contrast’ function of the PAT-GEOM software, which operates in IMAGEJ (Chan *et al.* 2019). PAT-GEOM is a software that allows users to measure various pattern features of interest from selected areas within photographs. Specifically, it was designed to measure biological patterns (Chan *et al.* 2019). A user guide and further information about PAT-GEOM and its applications can be found on the website of the creator: ianzwchan.com/my-research/pat-geom/. To obtain the PAT-GEOM contrast values (henceforth ‘contrast values’), each photograph was opened on full screen in IMAGEJ and nests were outlined at 1× zoom. Where branches or leaves intersected the visual of a nest, the largest uninterrupted section of a nest was outlined. Accordingly, the contrast values of the background were obtained from five random samples in each photograph. Each random sample of the background was pre-set in terms of size and shape (450 × 450, oval) with the ‘specify’ function in IMAGEJ. These steps resulted in 12 control nest samples, 12 treated nest samples and 60 random background samples for the green and brown natural nests each. For man-made brown nests, 10 control nest samples, 10 treated nest samples and 50 random background samples were obtained.

Statistical analyses

The collected predation and location data from Experiments 1 and 2 were analysed with binomial generalized linear mixed models (GLMMs) because the dependent variables in Experiments 1 and 2 were both binary; predicated/not predicated and located/not located, respectively. The contrast data from Experiment 3 were analysed with a linear mixed model (LMM) because the contrast values fitted a normal distribution. Random effects were introduced to the models to account for the fact that measurements were not fully independent (see below).

The fixed variables in Experiment 1 included treatment (control/treated), nest type (green/brown) and the interaction term between treatment and nest type. Random effects included nest pair ID and site ID, which were partly crossed. Crossed random effects occur when one level of a random effect appears in more than one level of another random effect (van den Bergh & Quené 2008). In other words, nest pair ID and site ID were partly crossed because some nest pairs were used in more than one site. The fixed variables in Experiment 2 were identical to those of Experiment 1. However, here nest type had three levels (green/brown/man-made brown). The random effects included subject ID (subjects 1–94) and subject group ID (group 1/group 2), which were nested. Random effects are considered nested when one level of a random effect only occurs in one level of another random effect (Ten Have *et al.* 1999). In other words, subject ID and group ID were considered nested because subjects in group 1 never occurred in group 2 and vice versa. The fixed variables in Experiment 3 included the sampled features (background/treated nest/control nest) and nest type (green/brown/man-made brown) and their interaction term. The only random effect variable was picture ID because adding nest pair ID as a random effect was redundant; each nest type (fixed effect) was represented by a single nest pair.

After assessment of the three full models containing all aforementioned variables, the interaction terms were removed if not significant. This ultimately resulted in three final models used in the analyses (one model per dependent variable). The final GLMM for Experiment 1 modelled the associations of treatment (fixed effect) and site ID (random effect) with odds of predation. The final

GLMM for Experiment 2 modelled associations of treatment (fixed effect), nest type (fixed effect), interaction of treatment and nest type (fixed effect) and picture ID (random effect), with odds of location. Because the effect of treatment was not the same for all nest types as indicated by their significant interaction, the effects of treatment (with picture ID as a random effect) on location were in turn individually analysed for each nest type with GLMMs. The final LMM for Experiment 3 analysed the contrast values in response to which features were sampled and the nest types (fixed effect), and picture ID (random effect).

The final models of the nest predation experiment (Experiment 1) and the visual search (Experiment 2) showed some evidence of being over-fitted. However, two identical models without the random effects yielded qualitatively similar outcomes (see Appendices 2 and 3 for Experiments 1 and 2, respectively). The observed overfitting was therefore unlikely to have been a problem in our analyses. Although we could have excluded the random effect variables based on the fact that they did not substantially enhance the statistical analyses, we instead opted to retain all of the aforementioned random effect variables to maintain a faithful representation of our experimental design. Notably, in the final model of Experiment 3, the contrast analysis was not overfitted.

RESULTS

Experiment 1: Nest predation experiment

Given the absence of a significant interaction between treatment and nest type, the nest type did not affect the effect of treatment on the odds of nests being predated. The final model demonstrated that the odds of predation were also not significantly affected by treatment or nest type ($n_{\text{Brown}_{\text{pairs placed}}} = 59$, $n_{\text{Green}_{\text{pairs placed}}} = 32$, $n_{\text{Control}_{\text{pred}}} = 24$, $n_{\text{Treated}_{\text{pred}}} = 25$; $Z = 1.17$, $P = 0.24$ and $n_{\text{Brown}_{\text{pred}}} = 31$, $n_{\text{Green}_{\text{pred}}} = 18$; $Z = -0.19$, $P = 0.85$, respectively). The predation rates experienced by control nests and treated nests (irrespective of nest type) were approximately equal at 26.4 and 27.5%, respectively. Predation rates experienced by brown and green nests (irrespective of treatment) were approximately equal at 29.0 and 26.3%, respectively.

Eggshells were occasionally found near predated nests. These eggshell remains always had a single puncture. Punctures were clean without severe cracking in the remainder of the shell. Moreover, scratches characteristic of rats and mice (Marini & Melo 1998) were not observed on any intact eggs or eggshell remains. Carrion Crows *Corvus corone*, Eurasian Jays *Garrulus glandarius* and Eurasian Magpies *Pica pica* were regularly observed in the vicinity of experimentation sites.

Experiment 2: Photo-based visual search experiment

Although the final model indicated that the effect of treatment on odds of location differed between the brown nest and the man-made brown nest ($Z = 6.03$, $P < 0.005$), the effect of treatment on odds of location in green and natural brown nests was not significantly different ($Z = -1.66$, $P = 0.10$).

Individual analyses of green and brown nests indicated that odds of location in treated nests were significantly lower than in controls (Green: $n = 562$, $n_{\text{Control}_{\text{loc}}} = 323$, $n_{\text{Treated}_{\text{loc}}} = 239$, $Z = -4.99$, $P < 0.005$; Brown: $n = 552$, $n_{\text{Control}_{\text{loc}}} = 298$, $n_{\text{Treated}_{\text{loc}}} = 254$, $Z = -2.65$, $P = 0.008$), where $n_{\text{Control}_{\text{loc}}} =$ no. of times non-treated control nests were located and $n_{\text{Treated}_{\text{loc}}} =$ no. of times treated nests were located. Conversely, for man-made brown nests the odds of the treated nests being located were significantly higher than the odds of the controls being located ($n = 457$, $n_{\text{Control}_{\text{loc}}} = 185$, $n_{\text{Treated}_{\text{loc}}} = 272$, $Z = 5.72$, $P < 0.005$; Fig. 1).

Experiment 3: Contrast analyses of photos using PAT-GEOM software in IMAGEJ

Due to the lack of a significant interaction between treatment and nest type in our final model, our results indicated that the effect of treatment on the contrast values of nests and the background (mainly foliage) did not differ between the three nest types. According to our model, the background contrast values of pictures with the man-made brown nests and the green nests did not differ significantly from those of the brown nests: $n_{\text{Background}} = 170$, $\text{df} = 8.42$, $t = 0.12$, $P = 0.91$ and $\text{df} = 8.42$, $t = -1.32$, $P = 0.20$, respectively, where $n_{\text{Background}} =$ no. of samples

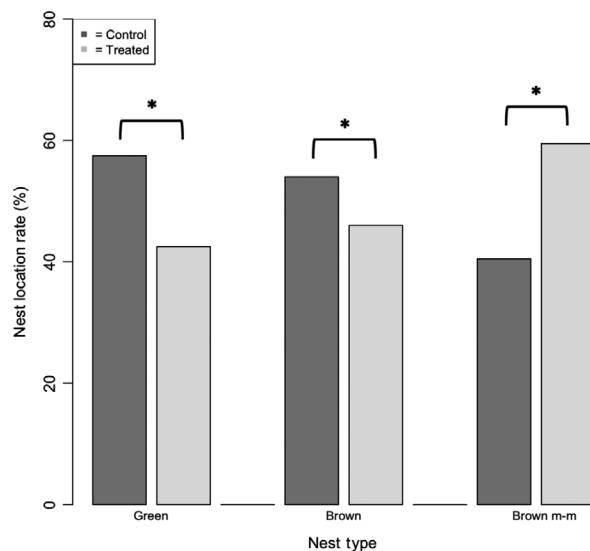


Figure 1. Location rates of treated and non-treated green, brown and man-made (m-m) brown nests. Control = non-treated nests. Treated = artificially treated nests. Brown m-m = brown man-made nests. Green: $n = 562$. Brown: $n = 552$. Brown m-m: $n = 457$. *Statistically significant difference at $P < 0.05$.

taken of the background. However, the contrast values of the control and treated nests did differ significantly from the background ($n_{\text{Treated}} = 34$, $n_{\text{Control}} = 34$, $n_{\text{Background}} = 170$, treated: $\text{df} = 14.93$, $t = 5.53$, $P < 0.005$. control: $\text{df} = 14.93$, $t = -3.88$, $P < 0.005$, where $n_{\text{Treated}} = \text{no. of samples taken of treated nests}$ and $n_{\text{Control}} = \text{no. of samples taken of control nests}$. Because the contrast values of the control and treated nests differed significantly from the background in opposite directions (i.e. treated nests had higher contrast values and controls had lower contrast values), statistical comparison of the control and treated nests was superfluous. Instead, we can safely infer that the contrast values of treated and control nests were significantly different, and that the contrast values of the treated nests were higher than those of the control nests (Fig. 2).

DISCUSSION

Artificial placement of nests in the experiments

The above-described methodology is not suitable for estimating absolute predation rates on nests. However, the randomized paired experimental

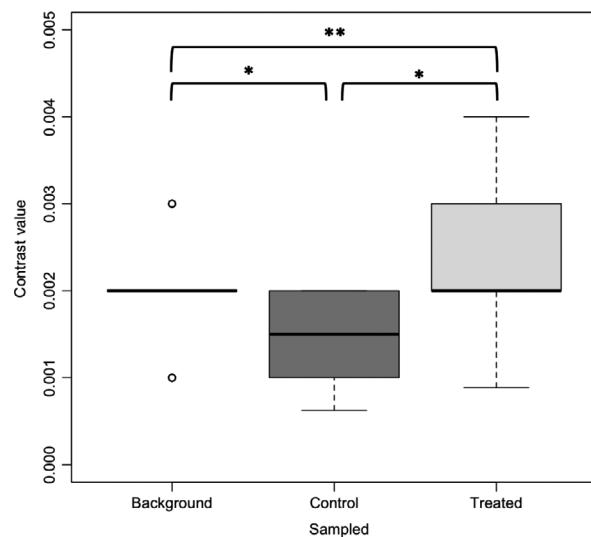


Figure 2. Contrast values of nests and random samples of the background. Control = non-treated nests. Treated = artificially camouflaged nests. Green: $n_{\text{Control}} = 12$, $n_{\text{Treated}} = 12$, $n_{\text{Background}} = 60$. Brown: $n_{\text{Control}} = 12$, $n_{\text{Treated}} = 12$, $n_{\text{Background}} = 60$. Brown m-m: $n_{\text{Control}} = 10$, $n_{\text{Treated}} = 10$, $n_{\text{Background}} = 50$. *Statistically significant difference at $P < 0.05$. **Significant difference inferred (see text).

design does ensure that nest location and size and any other nest traits are not confounding factors. Moreover, to avoid any potential excessive effects of nest placement on detection, the microhabitats in which nests were placed during our experiments closely mimicked those in which nests were found during the nest-collection phase.

Camouflaging effects on predation and location rates

The white objects in the nest predation experiment did not have a significant camouflaging effect. However, in the photo-based visual search experiment, the white objects on treated bird-made natural nests did indicate a camouflaging effect (Fig. 1). In contrast to the natural green and brown nests, the same white objects caused man-made brown nests to become more easily locatable than the controls.

Experiment 1 showed no effect of exterior nest manipulation on predation rates, whereas Experiment 2 strongly suggested that this manipulation made natural nests at least harder for humans to detect. The observed apparent discrepancy in terms of the camouflaging effects of white spots between Experiments 1 and 2 may be explained

by several factors. First, differences in results may have been caused by the different materials used in Experiments 1 and 2 to mimic white objects. However, the appearances of the liquid chalk spots and paper spots were comparably matt-white, with clearly defined edges. As such, the different materials probably do not explain the discrepancy in the results. Second, nest predators may have learned to locate nests regardless of camouflage by tracking the experimenter in Experiment 1, whereas the human subjects could not do so in Experiment 2. However, it is unlikely that such learning took place in Experiment 1 because there was minimal opportunity to associate the experimenter with food due to the irregular and random use of numerous and widely distributed experimentation sites. Third, nest predation in Experiment 1 could solely have been inflicted by olfactory predators, which are not affected by visual camouflaging, whereas the human subjects in Experiment 2 relied solely on visual cues. However, because various avian visual nest predators were regularly observed near test sites, it cannot be assumed that these animals did not predate the nests.

Furthermore, nest predation in Experiment 1 may have been inflicted by predators with different visual sensitivities from human subjects in Experiment 2. Indeed, during Experiment 1, the majority of predation was probably inflicted by avian nest predators. Lastly, we cannot discount the possibility that the significant effects found in Experiment 2 were type I errors. However, we do note in this regard that the larger sample size and reduced inherent variation in the design of Experiment 2 should translate into much higher statistical power.

Ultimately the findings of Experiment 2 suggest that adhering white material to some cup-nest exteriors may be an effective camouflaging strategy against visual nest predators with visual sensitivities comparable to that of humans, thus supporting Hansell's hypothesis (Hansell, 1996). Nonetheless, the predation observed in Experiment 1 also seems to indicate that this treatment is not completely effective against all visual nest predators.

Importance of contrast characteristics

White spots significantly increased the contrast of treated nests relative to controls for all nest types

(Fig. 2). Additionally, contrast values of nests were raised significantly beyond that of the background/surrounding foliage. In the case of natural nests, treated nests experienced lower location rates. It thus appears that the observed contrast increase may have had a camouflaging effect on natural nests through disruption. Conversely, the treated man-made brown nests with higher contrast values experienced significantly higher location rates than their control counterparts with lower contrast values. However, it is important to remember that we placed both brown and green nests in similar situations – it may be that they naturally occur in different types of locations – which may mitigate the effect discussed above.

Comparison of the contrast characteristics of nests and foliage, combined with the associated relative predation/location rates of Experiments 3 and 2, respectively, allowed us to pinpoint the types of camouflage that were probably at work. First, in the case of background contrast matching, one might expect background matching to be imperfect and so controls to differ from the background, and this difference to be reduced when nests are more challenging to find by visual search (Nokelainen & Stevens 2016). Contrary to this prediction, the mean contrast values of our brown modified nests were more different from the background compared with their control counterparts. Indeed, the contrast values of the non-treated controls of the natural green and brown nests were not significantly different from the background. Brown and green controls thus matched the background contrast and therefore theoretically already benefited from camouflage by way of background matching. Consequently, it is unlikely for white spots to be stuck to the exterior of nests. Note that the contrast values of neither the treated nor the control man-made brown nests matched those of the background contrast, and thus also do not support background matching.

Disruptive camouflage is different from background matching because it is inherently dependent upon relatively high contrasts to disrupt the silhouette of an object or animal (Nokelainen & Stevens 2016). Because background matching was not further improved by the adherence of the white spots in Experiment 2, but the significant contrast increase caused a significant reduction in location rates of natural nests, we can deduce that disruptive camouflage was at work.

Ultimately, our results indicate that white objects may be stuck to the exterior of green cup-nests to achieve disruptive camouflage in combination with background matching. However, our findings further suggest that birds should carefully increase contrast to achieve disruptive camouflage, while avoiding excessive contrasts which appear to be particularly detrimental for nest location. Avoidance of the latter may indeed be the reason why white objects are not stuck on brown nests in nature. Overall our results indicate that bird nest camouflage requires further scientific examination.

The authors are very grateful for the reviewers' invaluable insights into the project. We are additionally very appreciative of the critical suggestions offered by the Associate Editor (Dr Martínez-Padilla) and Editor (Dr Dan Chamberlain).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

- Bailey, I.E., Muth, F., Morgan, K., Meddle, S.L. & Healy, S.D. 2015. Birds build camouflaged nests. *Auk* **132**: 11–15.
- van den Bergh, H. & Quené, H. 2008. Examples of mixed-effects modeling with crossed random effects and with binomial data. *J. Mem. Lang.* **59**: 413–425.
- Chan, I.Z.W., Stevens, M. & Todd, P.A. 2019. PAT-GEOM: a software package for the analysis of animal patterns. *Methods Ecol. Evol.* **10**: 591–600.
- Ebay 2019. 10cm Handmade Vine Bird Nest House Sill Nature Craft Holiday Decoration. Ebay.co.uk.
- Gómez, J., Ramo, C., Troscianko, J., Stevens, M., Castro, M., Pérez-Hurtado, A., Liñán-Cembrano, G. & Amat, J.A. 2018. Individual egg camouflage is influenced by microhabitat selection and use of nest materials in ground-nesting birds. *Behav. Ecol. Sociobiol.* **72**: 1–10.
- Hansell, M.H. 1996. The function of lichen flakes and white spider cocoons on the outer surface of birds' nests. *J. Nat. Hist.* **30**: 303–311.
- Lovell, P.G., Ruxton, G.D., Langridge, K.V. & Spencer, K.A. 2013. Egg-laying substrate selection for optimal camouflage by quail. *Curr. Biol.* **23**: 260–264.
- Mainwaring, M.C., Deeming, D.C., Jones, C.I. & Hartley, I.R. 2014. Adaptive latitudinal variation in Common Blackbird *Turdus merula* nest characteristics. *Ecol. Evol.* **4**: 851–861.
- Marini, M.A. & Melo, C. 1998. Predators of quail eggs, and the evidence of the remains: implications for nest predation studies. *Condor* **100**: 395–399.
- Martin, T.E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* **65**: 101–127.
- Montgomerie, R., Lyon, B. & Holder, K. 2001. Dirty ptarmigan: behavioral modification of conspicuous male plumage. *Behav. Ecol.* **12**: 429–438.
- Nokelainen, O. & Stevens, M. 2016. Camouflage. *Curr. Biol.* **26**: 654–656.
- Ten Have, T.R., Kunselman, A.R. & Tran, L. 1999. A comparison of mixed effects logistic regression models for binary response data with two nested levels of clustering. *Stat. Med.* **18**: 947–960.
- Tinbergen, N., Broekhuysen, G.J., Feekes, F., Houghton, J.C.W. & Kruuk, H. 1962. Egg shell removal by the Black-Headed Gull, *Larus ridibundus* L.; a behaviour component of camouflage. *Behaviour* **19**: 74–117.
- Troscianko, J., Wilson-Agarwal, J., Stevens, M. & Spottiswoode, C.N. 2016. Camouflage predicts survival in ground-nesting birds. *Sci. Rep.* **6**: 1–8.
- Weidinger, K. 2001. Does egg colour affect predation rate on open passerine nests? *Behav. Ecol. Sociobiol.* **49**: 456–464.
- Westmoreland, D. & Best, L.B. 1986. Incubating continuity and the advantage of cryptic egg coloration to Mourning Doves. *Wilson Bull.* **98**: 297–300.
- Westmoreland, D. & Kiltie, R.A. 1996. Egg crypsis and clutch survival in three species of blackbirds (Icteridae). *Biol. J. Linn. Soc.* **58**: 159–172.
- Wilson-Agarwal, J.K., Troscianko, J.T., Stevens, M. & Spottiswoode, C.N. 2016. Escape distance in ground-nesting birds differs with individual level of camouflage. *Am. Nat.* **188**: 231–239.

Received 27 June 2019;
revision accepted 29 April 2020.

Associate Editors: Jesus Martínez-Padilla and Dan Chamberlain.

APPENDIX 1

Photograph of a man-made nest as advertised online (Ebay 2019). Supplied by Sill Nature Craft Holiday Decoration. Link to the advertisement: www.ebay.co.uk/itm/123092989138

**APPENDIX 2**

Association of nest type and treatment with odds of nest predation in final models without random effect variables

	logOR (± 1 se, <i>P</i> -value), model 1*	logOR (± 1 se, <i>P</i> -value), model 2**
Fixed effect		
Nest type		
Brown	Ref	Ref
Green	0.09 (± 0.35 , <i>P</i> = 0.27)	0.51 (± 0.44 , <i>P</i> = 0.24)
Treatment		
Control	Ref	Ref
Treated	0.06 (± 0.33 , <i>P</i> = 0.17)	0.07 (± 0.07 , <i>P</i> = 0.85)

OR, odds ratio; Ref, reference group; se, standard error.
*Model 1: general linear model including nest type and treatment as fixed effects. **Model 2: generalized linear mixed model including nest type and treatment as fixed effects in addition to site ID and pair ID fitted as random effects.

APPENDIX 3

Association of nest type, treatment and their interaction with odds of nest location in final models without random effect variables

	logOR (± 1 se, <i>P</i> -value), model 1*	logOR (± 1 se, <i>P</i> -value), model 2**
Fixed effect		
Nest type		
Brown	Ref	Ref
Brown m-m	−0.55 (± 0.13 , <i>P</i> < 0.005)	−0.55 (± 0.13 , <i>P</i> < 0.005)
Green	0.14 (± 0.12 , <i>P</i> = 0.24)	0.14 (± 0.12 , <i>P</i> = 0.24)
Treatment		
Control	Ref	Ref
Treated	−0.32 (± 0.12 , <i>P</i> = 0.008)	−0.32 (± 0.12 , <i>P</i> = 0.008)
Treatment * Nest type		
Treated	Ref	Ref
Brown		
Treated	1.09 (± 0.18 , <i>P</i> < 0.005)	1.09 (± 0.18 , <i>P</i> < 0.005)
Brown m-m		
Treated	−0.28 (± 0.17 , <i>P</i> < 0.005)	−0.28 (± 0.17 , <i>P</i> < 0.005)
Treated Green		

Brown m-m, brown man-made nests; OR, odds ratio; Ref, reference group; se, standard error. *Model 1: general linear model including nest type, treatment and their interaction term as fixed effects. **Model 2: generalized linear mixed model including nest type, treatment and their interaction term as fixed effects, as well as group ID and subject ID as random effects.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Experiment 1: *in situ* nest predation data.

Data S2. Experiment 2: photo-based visual search data.

Data S3. Experiment 3: contrast analyses data.