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RESEARCH PAPER

Egg rejection from dark cavities: compensation for chromatic changes in nest illumination by a cuckoo host

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Abstract. Rejection of foreign eggs is an effective defence against brood parasitism in birds. Colourful egg stimuli are among the most important cues for recognition, but varying ambient light conditions can potentially affect the decision-making process. Birds may compensate for varied illumination through colour constancy, but this remains untested in brood parasite hosts. This ability may aid in recognising foreign eggs in the nest by making the decision process more robust and reliable. We examined if ambient light colour impacts the rate at which the common redstart (*Phoenicurus phoenicurus*) rejects white egg models while keeping foreign-host egg contrast consistent. The cavity-nesting redstart is host to the common cuckoo (*Cuculus canorus*) and exhibits colour-biased egg rejection behaviour under natural light, where they preferentially reject eggs that they perceive as browner than their own eggs but, in contrast, accept eggs that they perceive as bluer than their own. Under the colour constancy hypothesis, we predicted that their responses towards the white egg would be similar between different light conditions. On the other hand, if redstarts lack colour constancy, their responses will differ between light conditions. No difference was found among rejection rates, suggesting that redstarts most likely base decisions on perceived differences between foreign and their own eggs while compensating for changes in illumination. These results imply that perceptual mechanisms like chromatic adaptation do not drive redstart colour-biased rejections. Further study on colour constancy in open and closed-nesting species will clarify illumination effects on parasite-host coevolution.

Key words: brood parasitism, colour constancy, egg discrimination, common redstart, common cuckoo, bird vision

Introduction

Recognition is a central process in the coevolutionary arms races between avian brood parasites and their hosts (Soler 2017). One highly effective way to avoid the costs of parasitism is to reject recognized parasitic eggs (Rothstein 1990, Feeney et al. 2014). Indeed, some hosts have evolved recognition abilities so refined that they have arguably won the co-evolutionary struggle with their parasites (Honza et al. 2004).

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On the other hand, some parasites have evolved highly accurate eggshell mimicry so that their eggs are nearly indistinguishable from their hosts (Igic et al. 2012). Ultimately, coevolved eggshell mimicry often displays ever-improved colour and maculation because hosts commonly use these traits to recognize a parasite egg (Honza & Cherry 2017, Samaš et al. 2021).

Hosts are expected to recognize parasite eggs based on the perceivable difference in colour between parasite eggs and their own eggs; however, recent studies show that hosts may not reject foreign eggs based on the total degree of dissimilarity in colour (Hanley et al. 2017). Instead, many hosts preferentially reject eggs that appear browner than their own eggs and accept eggs that appear bluer than their own (Hanley et al. 2017, 2019, Abolins-Abols et al. 2019, Manna et al. 2020). These findings may open intriguing possibilities for the coevolutionary processes that give rise to mimicry, but we currently do not know the underlying mechanism that explains these findings over the taxonomic, ecological, and geographic breadth across which these tests were replicated. While some cognitive processes like generalization (Ghirlanda & Enquist 2003, ten Cate & Rowe 2007) or categorization (Caves et al. 2018) may explain these behaviours (Hanley et al. 2021), other perceptual processes may provide simpler solutions (Hanley et al. 2021). It is important to rule out these simpler explanations before investigating the more complex cognitive processes (e.g. categorization). Here, we use these counter-intuitive experimental findings to explore one simple feature of host visual machinery: the colour constancy ability.

We typically assume that birds possess colour constancy, which is the ability to consistently perceive colourful stimuli irrespective of the colour of illumination (Hurvich 1981, Lind 2016, Kelber et al. 2017, Kelber 2019); however, deficiencies in this ability could easily explain colour-biased egg rejection if hosts nest under variable illumination conditions. Indeed, colour constancy is sometimes imperfect, and specific illumination conditions may derail this process (Chittka et al. 2014, Olsson et al. 2016, Escobar-Camacho et al. 2019). Thus, it is crucial to assess a host's colour constancy ability. An animal's colour constancy ability can be tested by monitoring its performance on standardized colour discrimination tasks under distinct illumination conditions (e.g. Escobar-Camacho et al. 2019). Specifically, testing the colour constancy in an avian brood-parasite host would require researchers to manipulate the perceived colour of a parasitized clutch by varying nest illumination and determine whether specific light conditions yield specific responses. Consistent performance on the egg rejection tasks suggests that hosts have colour constancy, while differences in performance suggest that hosts lack colour constancy. Such tests would prove challenging for open-nesting species.

Here, we tested the effect of illumination colour on the egg rejection abilities of a cavity-nesting host, the common redstart (*Phoenicurus phoenicurus*; hereafter, redstart). To do so, we manipulated the colour of ambient light within redstart nests to test whether they would treat an experimentally introduced white egg model differently under different lighting conditions. Previous research has found that redstarts are more likely to reject brown eggs than equally dissimilar blue eggs (Manna et al. 2020); however, unlike most hosts that display a colour-biased rejection behaviour, redstarts are cavity-nesting species (but see Di Giovanni et al. 2023). These circumstances allowed us to experimentally alter ambient colour using three experimental treatments with coloured light-emitting diode lights (hereafter LED). Specifically, we adjusted the lighting conditions to be browner, bluer, or neutral (white) while also including a no-LED-light control treatment. Thus, the appearance of the white foreign eggs would vary, yet the relative differences between eggs would be relatively consistent. If redstarts possess colour constancy, we predicted their responses to the white egg would be similar under different light conditions. Alternatively, if redstarts lack colour constancy, we predicted their responses to the white egg will differ between different light conditions. Based on previous findings, the redstart should reject more experimental eggs that will be illuminated by brown light, even if the perceivable difference to their own eggs was similar to the egg model illuminated by blue light.

Material and Methods

Experimental design

We monitored redstart nest boxes near Hodonín (48°56′ N, 17°15′ E) in the Czech Republic from May 6 to July 2, 2022. The forest stands of the study site are dominated by Scots pine (*Pinus sylvestris*), with an admixture of other tree and shrub species. The redstart is the only regular cavity-nesting cuckoo host that rejects non-mimetic foreign eggs (Fig. 1; Samaš et al. 2016). Cuckoo females laying beige and speckled eggs have recently parasitized our study population, with an incidence rate of about 4% between 2018 and

2023. This host represents a suitable model species for our study because previous knowledge suggests that the redstart can reject differently coloured and sized experimental eggs at various rates (Table 5 in Samaš et al. 2016, Manna et al. 2020, Honza et al. 2022). Our study population bred in approximately three hundred nest boxes mounted on tree trunks at a height of about 1.3-1.6 m. Nest box inner dimensions were 16 cm × 11 cm × 33 cm (depth, width and height), with the entrance hole 7 cm wide. Importantly, the enclosed cavity environment allowed us to manipulate light in the nest efficiently without significant contamination by daylight. Although these dark cavities can represent a more challenging environment for recognising foreign eggs, Honza et al. (2022) suggested that redstarts have adequate illumination in their nests for egg discrimination tasks (see also Yang et al. 2022). Redstarts rejected foreign eggs at similar rates even after researchers experimentally decreased the natural light intensity inside their nest boxes.

On the first day of incubation in the redstart, we installed a nest box extender, which was a modified wooden roof case 8.5 cm deep, joined to the nest box body and containing a preinstalled LED device in a plastic pot (height 6.9 cm, bottom diameter 6.6 cm, top diameter 8.9 cm) covered with a light diffuser made from baking paper (Fig. 1). The plastic pot was attached to the adapter using a hook-and-loop fastener and its interior side was entirely covered by white paper to ensure the colours were reflected uniformly. Screws attached a special wooden thin-walled adapter over each nest box entrance hole to reduce the entrance diameter from 7 to 3.5 cm, which decreased the nest box interior average illuminance from approx. 65 lux to approx. 25 lux (Table 1 in Honza et al. 2022). This design decreased contamination by natural daylight and improved the conditions for light manipulation.

The next day, between 7-8 a.m., we added a white egg model into the nest and, in experimental nests (see below), turned on the LED device (golight submersible LED light from Amazon.de) pointing to the nest cup. The white egg model dimensions were similar to the common cuckoo eggs, with a mean weight of 3.4 g, a length of 22.0 mm, and a width of 17.3 mm (n = 8). Importantly, the UV reflectance of the egg models was also similar to the host eggs (see ‘control egg’ in Fig. 1 in Honza et al. 2022), and previous studies suggested that the white eggs are rejected at a moderate rate (Dinets et al. 2015, Honza et al. 2022). Also, we used a white colour for the experimental egg because it reflects most of the visible spectrum of light and thus takes on the colour of the

Fig. 1. Example of a white egg model rejected on the nest rim (white arrow). The inset shows an LED light mounted to a nest box roof extender with an LED device placed inside a plastic pot and covered by a diffuser.

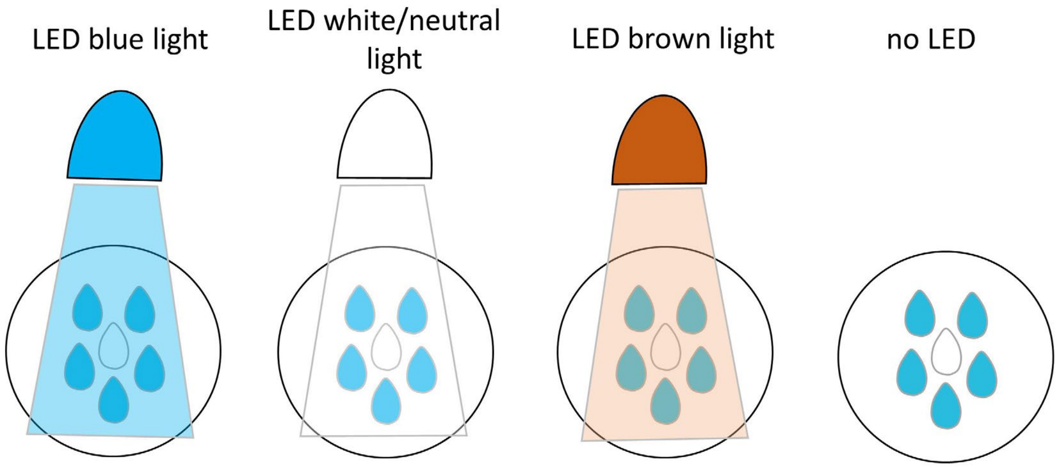

Fig. 2. Schematic illustrating the experimental LED treatments with a single white egg model alongside five blue host eggs.

LED light source. We randomly assigned each nest to one of the three LED colour treatments, brown, blue, or white, or assigned nests as a control (Fig. 2). In the control treatment, we only introduced a single white egg model into the nest without LED (no-LED-light) and nest box extender, which enabled us to estimate baseline rejection rates of the white egg model under natural light conditions. Each treatment lasted five days after the white egg model was introduced. If the nest was still active (eggs were incubated) and the artificial egg was still in the nest cup on the sixth day, the host female was deemed an acceptor. If the artificial egg disappeared from the box or was found outside the nest cup inside the box (Fig. 1) within those five days, the experiment ended, and the host female was deemed a rejecter (see Manna et al. 2020). Each nest was checked twice daily, between 7-8 a.m. and 7-8 p.m.

We also examined the possibility that the experimental LED setup represents a noticeable stressor for breeding redstarts. We used an LED setup with installed but non-operating LEDs (no light generated) and without an egg model introduced into the nest. This treatment was imposed on the nest for the same observation period, at the same breeding stage and

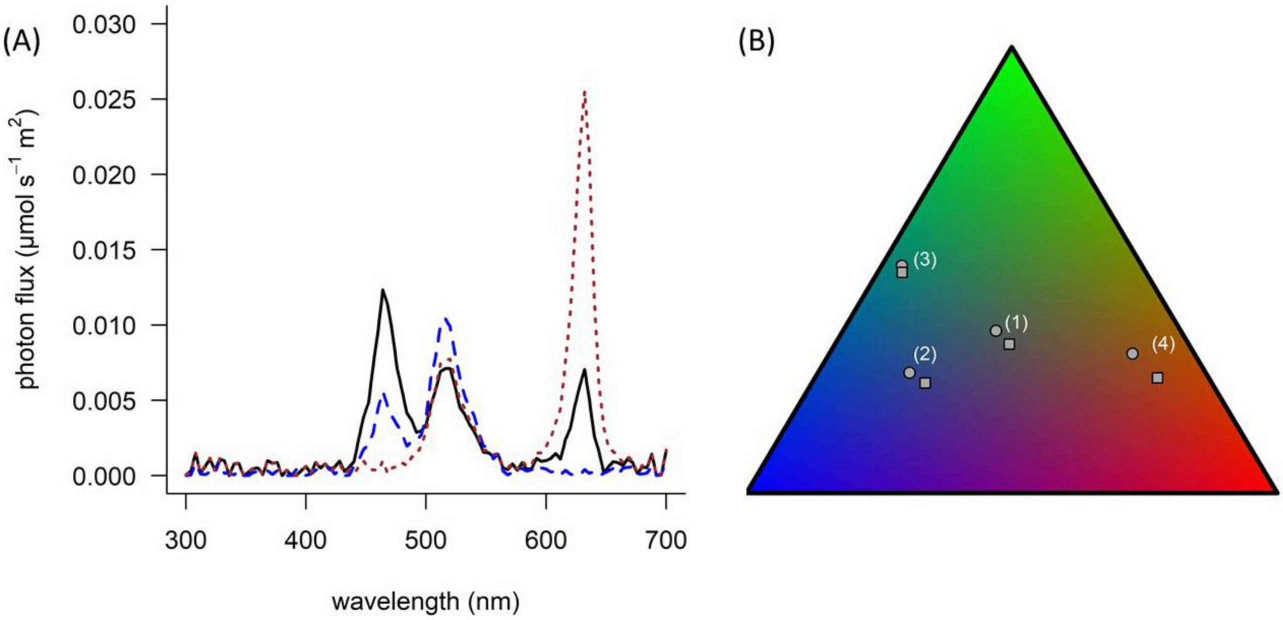

Fig. 3. We used three distinct settings on the LED device to produce (A) light that was 'white' (solid black lines), 'blue' (dashed blue line), and 'brown' (dotted brown line). These light conditions dramatically impacted the (B) chromaticity coordinates of the redstart and foreign white eggs (grey circles and squares, respectively) within the avian tetrahedral colour space. Here, we illustrate the tetrahedral colour space from a vantage point above the vertex representing the stimulation of the ultraviolet photoreceptor, thus oriented directly on the plane defined by birds' other three photoreceptors. The chromaticity coordinates are (1) plotted ignoring light (assuming an idealized light source), and under the (2) white, (3) blue, and (4) brown LED.

in the same way as in the experimental setup. Out of 11 examined nests, no nest was abandoned, and we concluded that our setup was not a significant stressor to the redstarts.

Light and colour quantification

Each LED unit allowed for 16 different light settings at ten brightness levels (1 = dimmest, 10 = brightest). In this case, we used the white LED light setting at brightness level 2, the blue-green LED light (the button immediately below the 'G' button) on brightness level 3, and the red-orange LED light (the button immediately below the 'R' button) on brightness level 9. Although the levels differed, the measured light intensity was similar among the three light settings (66, 69, and 73 lux for white, blue, and brown, respectively). We quantified the absolute irradiance following Appendix A of Johnsen (2012). Each light setting was measured within the same cup apparatus in the dark using a recently radiometrically calibrated spectrometer (USB 4000, Ocean Optics, Dunedin, FL, U.S.A.) at 23 cm (Fig. 3).

Then, we used avian visual models to quantify the colours of the redstart and white experimental eggs used in this experiment. These analyses relied on reflectance spectra of the average redstart egg from this population and the white experimental egg from a previous study (see Fig. 1 in Honza et al. 2022). These were measured using a JAZ reflectance spectrometer with an in-built PX3 pulsed xenon light source (JAZ Spectrometer, Ocean Optics, Dunedin, FL, U.S.A.) and calibrated to a diffuse 98% white standard (WS-2, Avantes BV, NL). We calculated the quantum catches associated with how hosts view the natural redstart and experimental egg using the following equation

$$Qi = \sum_{300}^{700} R_i\,(\lambda)\,O\,(\lambda)\,S\,(\lambda)\,I\,(\lambda)$$

where R_i refers to the sensitivity of photoreceptor i for the average ultraviolet-sensitive avian viewer (Endler & Mielke 2005), O refers to the oil transmission in this case for the blue tit *Cyanistes caeruleus* (Hart et al. 2000), S refers to the spectral reflectance (see above), and I refers to the illumination converted to photon flux units (µmol s^{-1} m^2). These calculations were repeated for the three distinct experimental light treatments, using the 'vismodel' function in the R package 'pavo' (Maia et al. 2019).

We then used a receptor noise limited model (Vorobyev & Osorio 1998) to determine how noticeable the foreign white egg would appear compared to the redstart's own eggs under each of the three light conditions. This approach assumed the relative cone densities of the blue tit (Hart et al. 2000) and receptor noise of 0.1 for the long wavelength sensitive photoreceptor (Olsson et al. 2018). This approach produced metrics of visible contrast in just noticeable differences where a value below one would not be noticeable, a value of one would be just noticeable (under ideal conditions), and values increasingly above one would be increasingly noticeable. We also estimated perceived differences in brightness using quantum catch estimates using double cone sensitivities of the blue tit (Hart et al. 2000) and receptor noise of 0.2 (Olsson et al. 2018). These calculations used the 'coldist' function in the R package 'pavo' (Maia et al. 2019). We calculated luminance contrast using a derivation of the receptor noise-limited model intended for monochromatic viewers (Siddiqi et al. 2004) and also by calculating Michelson contrasts (Peli 1990), following Olsson et al. (2016). Specifically, we calculated Michelson contrasts as

$$\frac{Q_{\text{white model}} - Q_{\text{redstart}}}{Q_{\text{white model}} + Q_{\text{redstart}}}$$

where $Q_{\text{white model}}$ and Q_{redstart} represent the double cone quantum catch for the white egg model and the natural redstart egg, respectively. Finally, we calculated the chromaticity coordinates within the tetrahedral colour space (Stoddard & Prum 2008) for each egg (redstart and model) under each of the three experimental light regimes, using the 'colspace' function in the R package 'pavo' (Maia et al. 2019). Here, we expect that chromatic and achromatic contrasts should be large enough to be detectable by birds (> 2 JND, > 0.15 Michelson Contrasts) but broadly similar for all treatments (Table 1), yet the fundamental colours would be altered. Thus, if birds respond strongly to a particular colour, their responses could be attributed to the perceived colour of the foreign egg rather than the perceived contrast *per se*.

Statistical analysis

All the analyses were performed using the statistical software R v. 4.1.3 (R Core Team 2022). To determine whether light regimes significantly impacted host rejection, we ran a generalized linear model with binomial distribution and logit link to test effects of treatment (categorical; four LED settings; Fig. 2) and date of experimentation (continuous; ordinal date in the year) on egg rejection (binary; egg model accepted

Table 1. Summary table and statistics for the four experimental treatments for the samples, response to the artificial egg and contrast in just noticeable difference unit (JND) between artificial and host eggs.

Treatment	Egg only	Egg + LED white	Egg + LED blue	Egg + LED brown
n total	10	10	11	10
n ejected	2	1	0	1
n deserted	0	0	1	0
Rejection rate	0.20	0.10	0.09	0.10
Lower 95% CI	0.03	0.00	0.00	0.00
Upper 95% CI	0.56	0.45	0.41	0.45
chromatic contrast (JND)	4.55	4.72	3.99	4.98
achromatic contrast (JND)	4.05	3.83	3.52	4.26
Michelson contrast	0.38	0.37	0.34	0.40

or rejected). Rejection cases included foreign eggs ejected from the nest cup and one desertion case. We included desertion in the analyses because it is a type of response to real cuckoo parasitism (Thomson et al. 2016). Nevertheless, the significance of this particular response to experimental parasitism remains uncertain (Samaš et al. 2016, Honza et al. 2022). Therefore, we re-analysed the data with the desertion case excluded, and the conclusions remained the same (results not shown). After running a statistical model, we conducted diagnostics of model residuals using methods implemented in the R package DHARMa (Hartig 2022). These diagnostics included visual inspection of simulated residuals with Q-Q plots and goodness-of-fit simulation-based distribution test (degree of uniformity of the residuals), dispersion test (presence of under- or overdispersion in the residuals) and outlier test (presence of outliers in the residuals). Finally, we performed pairwise comparisons of model-adjusted marginal means (odds ratios) using the R package emmeans (Lenth 2022).

We originally intended to account for nest box orientation (in degrees; 0-360°) in the analyses. Nevertheless, the full model, which included the circular variable, exhibited poor convergence.

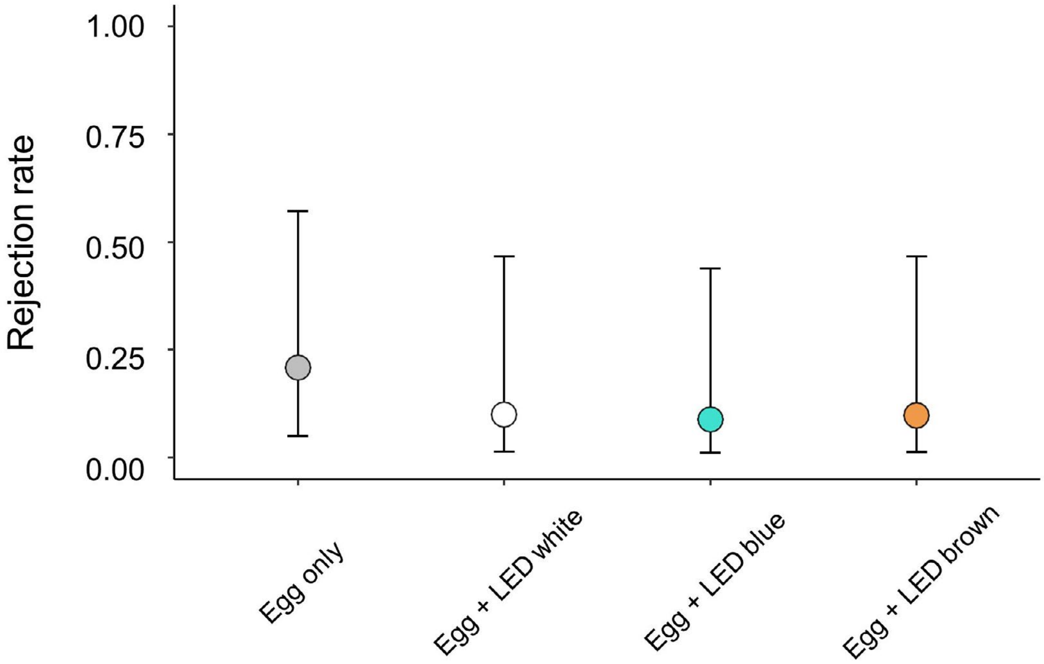

Fig. 4. Predicted means and 95% confidence intervals of rejection rates under four experimental treatments. Means and confidence intervals were predicted using a binomial linear model with a binary response variable (0 = artificial egg rejection, 1 = acceptance).

Table 2. Pairwise comparisons among the four experimental treatments. Statistics is derived from a binomial linear model with a binary response variable (0 = artificial egg rejection, 1 = acceptance).

contrast	Odds ratio	SE	z-ratio	*P*-value
Egg only/Egg + LED white	2.39	3.24	0.64	0.92
Egg only/Egg + LED blue	2.72	3.76	0.72	0.89
Egg only/Egg + LED brown	2.44	3.36	0.65	0.92
Egg + LED white/Egg + LED blue	1.14	1.70	0.09	1.00
Egg + LED white/Egg + LED brown	1.02	1.52	0.01	1.00
Egg + LED blue/Egg + LED brown	0.90	1.33	–0.07	1.00

Therefore, we present only results without considering this problematic predictor. The analysis with predictor 'direction' modelled, but excluding the effect of treatment, fitted well using the function gam from the package mgcv (Wood 2022). The outputs obtained were $P = 0.78$ for the variable 'direction' and $P = 0.99$ for the variable 'date'. This result implies that the 'nest box orientation' variable may not significantly impact rejection rates in the final analyses.

Our study population was not colour-banded, so we cannot exclude that we experimented on the same individual more than once; therefore, we employed techniques to reduce the potential risk of pseudoreplication (Hurlbert 1984). Specifically, we significantly reduced this risk by i) excluding second nest attempts by the redstart in the same nest box (n = 3) and ii) performing all experiments within a short time window of 43 days when most individuals were only about to accomplish their first breeding attempt.

Results

We detected similar rejection rates of 20% (n = 10), 10% (n = 10), 9% (n = 11), and 10% (n = 10) for the experimental treatments of egg model only (control), egg model with white LED, egg model with blue LED, and egg model with brown LED, respectively. Both predictors, type of treatment (LED setting) and date of experimentation, were non-significant ($P = 0.86$ and 0.83, respectively) (Table 1, Fig. 4). There were no differences between treatments when compared pairwise (Table 2).

Discussion

We have long known that hosts of avian brood parasites use colour as a vital cue in egg recognition (Samaš et al. 2021). Here, we experimentally manipulated light within the cavity to be brown, blue, or white using remote-controlled LED sources in a cavity-nesting brood-parasite host, the common redstart. Previous research has shown that this host species rejects eggs that they perceived as browner than their own (Manna et al. 2020). A range of host species exhibit this behaviour, including other cavity-nesting birds (Hanley et al. 2017, 2019, Abolins-Abols et al. 2019, Manna et al. 2020, Di Giovanni et al. 2023). These experiments raise interesting questions about the perceptual and cognitive bases of such behavioural responses (Hanley et al. 2021). Contrary to previous findings obtained through direct manipulation of egg colours, we found similar egg rejection rates across all notably different ambient light conditions. This result suggests that the redstarts may compensate for changes in the nest illumination, providing evidence for colour constancy. Additionally, our findings reinforce previous findings that have found rejection decisions are often based on the relative differences between the foreign egg and its clutch (Cassey et al. 2008, Spottiswoode & Stevens 2010; but see Hauber et al. 2020).

The importance of nest natural illumination on egg rejection has received mixed support, with some studies reporting that natural illumination significantly impacted host response (Avilés et al. 2006, Antonov et al. 2011), while others did not (Honza et al. 2011, Avilés et al. 2015, Medina & Langmore 2019). For example, Honza et al. (2022) recently found no difference in egg rejections in the redstart after experimentally decreasing nest illuminance by half. In this case, hosts performed similarly in dimmer conditions, suggesting light was adequate for egg discrimination. The study by Yang et al. (2022) also investigated the effect of nest illumination on egg rejection behaviour in the cavity-nesting green-backed tit (*Parus monticolus*). Under normal and moderately reduced luminance (38 and 5 lux, respectively), the rejection rate remained 100%. However, with a strongly reduced luminance of 0.4 lux, the rejection rate dropped to 0%. Their results showed that the ability to reject foreign eggs persisted under dim conditions but disappeared in near-total darkness. These findings also suggest that adverse weather conditions like cloud cover and precipitation may not substantially impact recognition abilities. In such weather, the diffuse skylight passing through the fixed-positioned entrance can be reduced, but at least some cavity-nesting species still have enough light to discern foreign eggs (Honza et al. 2022, Yang et al. 2022). Using a white/neutral LED light in this study directly increased the light intensity within our redstart boxes. However, this change in the light intensity did not affect the rejection rates of egg models. This finding supports a finding by Honza et al. (2022) that the light intensity of the nest environment has relatively low importance for parasitic egg rejection in the redstart and some other species breeding in enclosed nests (e.g. Honza et al. 2014). Additionally, our 'egg only' treatment replicated the previous experimental design of Honza et al. (2022) using the same egg model in the same population. We observed a similar pattern in the rejection rates between the studies (six out of 29 versus two out of ten; Fisher's exact test, $P = 1$). While the sample size of ten nests per treatment in our study is relatively small, the consistency in rejection rates between studies provides some confidence in the representativeness of the estimates. Obtaining matching rejection rates also suggests this can be a stable response for this species. While the consistency between studies offers some validation, it is important to remain cautious about making definitive claims and drawing informed conclusions based on modest samples.

Our findings suggest that redstart egg rejection decisions likely rely on relative colour comparisons between their own and foreign eggs. These comparisons are often modelled using a psychophysical model, such as the receptor noise-limited model (Vorobyev & Osorio 1998). Although ambient light conditions play a crucial role in colour perception (Endler 1990), precise measurements of nest light conditions are rarely known. However, we often assume that animals can compensate for varied ambient light through colour constancy (Kelber 2019). Accordingly, our experimental results provide support for this hypothesis. Unfortunately, the underlying mechanisms of colour constancy are not yet clear; however, it seems likely that animals adapt (*sensu* chromatic adaptation rather than evolutionary adaptation) to both the illumination and nest backgrounds (Renoult et al. 2015; but see Aidala et al. 2015, 2019). Future research should more fully explore the mechanisms of colour constancy and background contrast to better understand avian vision (Hanley et al. 2021).

It is becoming increasingly clear that cavity-nesting birds have visual systems well-tuned for decision-making in the dark (Chaib et al. 2023, Di Giovanni et al. 2023). Thus, it is no surprise that ambient natural light conditions have little impact on the redstart's ability to recognize parasitic eggs (Honza et al. 2022). Current knowledge thus supports the view that foreign egg detection is based primarily on identifying relative differences between the foreign egg and the host's clutch (Cassey et al. 2008); this study reinforces that view. Manipulating ambient light colour and chromatic contrasts between experimental and own eggs within a single study could further disentangle their roles in hosts' decisions to reject a parasitic egg.

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Author Contributions

P. Samaš, D. Hanley and M. Honza designed the study. M. Capek and O. Mikulica collected the data. P. Samaš, D. Hanley, C.H. Greenberg, L. Pistone and M. Capek analysed the data. All the authors wrote the manuscript. The authors declare that they have no conflict of interest.

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