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Source: Journal of Vertebrate Biology, 70(1)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.20111

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Journal of Vertebrate Biology

Open Access

J. Vertebr. Biol. 2021, 70(1): 20111 DOI: 10.25225/jvb.20111

RESEARCH PAPER

The blunt pole is not a source of more salient recognition cues than the sharp pole for the rejection of model eggs by American robins (*Turdus migratorius*)

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Received 2 October 2020; Accepted 27 October 2020; Published online 10 December 2020

Abstract. Hosts of obligate avian brood parasites can reduce the costs of raising parasitic offspring by rejecting foreign eggs from their nests. Rejecter hosts use various visual and tactile cues to discriminate between own and foreign eggs. The blunt pole hypothesis specifically states that avian-perceivable visual information at and around the broader pole of the eggshell contains more salient recognition cues than does the sharp pole of the same egg. The directional prediction is, therefore, that eggs painted non-mimetically on their blunt pole should more likely be rejected relative to those similarly painted on their sharp pole. This hypothesis had been experimentally tested and its predictions supported solely in mimetic avian host-parasite systems, with hosts producing denser and more variable eggshell maculation patterns at the blunt pole, and in one species with immaculate eggs but still with distinctly discernible blunt-pole specific colouration. Here we aimed to expand upon these previous works and assessed whether the blunt pole of model eggs contains more salient egg rejection cues, relative to the sharp pole, for the American robin (*Turdus migratorius*), a robust rejecter of non-mimetic brown-headed cowbird (*Molothrus ater*) eggs. In this system host eggs are uniformly immaculate whereas the brood parasitic shell is maculated. We painted model cowbird-sized eggs on either the blunt or the sharp half to mimic the immaculate robin egg colours and the other half to resemble non-mimetic egg colours and patterns. There was no statistical support for the predicted outcomes of the blunt pole hypothesis in our trials as rejection rates were similar regardless of whether eggs were painted with non-mimetic colours on the blunt or sharp poles. Future work should test the role of asymmetrical signalling content for anti-parasitic rejection of eggs in additional host species, especially those with both immaculate own and mimetic parasitic eggs.

Key words: egg ejection, host-parasite systems, recognition systems

Introduction

Recognition systems function best when reliable cues exist for the discrimination of salient traits and the identification of relevant classes of stimuli (Bradbury & Vehrencamp 1998). Within the context of avian host-parasite arms-races (Davies 2000), many hosts reduce the fitness losses associated with brood parasitism by recognizing and eliminating foreign eggs from the nest.

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Which sensory cues hosts use to discriminate own *vs.* other eggs has been the subject of a vast experimental literature (reviewed in Moskát et al. 2008, Sealy & Underwood 2012, Manna et al. 2017), and points to the use of visual (e.g. Stoddard & Hauber 2017) and tactile (Tosi-German et al. 2020), but not olfactory (Soler et al. 2014), shell traits to recognize parasitic eggs.

To increase the efficiency of communication systems, many receivers use partial, short-cut, or rule-of-thumb approaches to subsample the totality of the available information (Bradbury & Vehrencamp 1998). Accordingly, some hosts of con- or heterospecific brood parasitic birds, rely more heavily on colouration and maculation information generated by the blunt pole (Zolei et al. 2012) of avian egg shapes that are typically asymmetrical between the two ends of the long-axis (Stoddard et al. 2017). This appears adaptive because the blunt pole of many bird species' eggs is often more heavily and variably maculated than the sharp pole, implying richer and, perhaps, more reliable information content for own *vs.* other egg recognition contexts (Polačiková et al. 2007, 2011). Accordingly, experimental studies demonstrate that the manipulation of the appearance of the hosts' own eggs on the blunt pole half increases egg rejection rates more than on the sharp pole half (e.g. Polačiková & Grim 2010, Polačiková et al. 2010, Wang et al. 2020; Table 1).

However, to date, all such experimental studies have focused on hosts of brood parasites where the foreign eggs are, by definition (e.g. through the shared similarity of conspecific eggs) or co-evolutionarily (e.g. interspecific host-parasite arms-races), mimetic of the hosts' own eggs (Table 1). Furthermore, in all prior study species both with maculated (Polačiková & Grim 2010, Polačiková et al. 2010) or immaculate eggs (Wang et al. 2020), there was a discernible difference in the appearance of the blunt *vs.* sharp poles of natural eggs (Table 1). Here, instead, we studied the egg rejection propensities of American robins (*Turdus migratorius*; laying immaculate blue eggs without discernible blunt pole appearance: Croston & Hauber 2015; Fig. 1). The robin is a robust egg rejecter host of the non-mimetic eggs of brown-headed cowbirds (*Molothrus ater*; laying whitish, speckled eggs: Fig. 1) in North America (Rothstein 1982). In contrast to previous findings, we expected that the blunt pole hypothesis would not apply to robins both because their eggs lack pole-specific colour differentiation

Fig. 1. Naturally parasitized American robin nest with a brown-headed cowbird egg in Urbana, IL, USA; insets on the right: experimental clutches with the four different model egg types (photo Mark E. Hauber and Jeffrey P. Hoover).

and because the vast differences in the colouration and patterning of parasitic cowbird eggs from the robin eggs would overwhelm any sensory bias toward one eggshell pole or the other. Therefore, we predicted that model eggs painted as non-mimetic on either the blunt pole or sharp pole half of the egg would be rejected at statistically similar rates.

Material and Methods

During May-June 2020, we located active nests of American robins, with permission, throughout private gardens, orchards and tree farms near Urbana, IL, USA (for details of the study site and search methods, see Hauber et al. 2020a). American robins reject most non-mimetic model eggs at this site, and are also naturally parasitized on occasion by brown-headed cowbirds (Abolins-Abols & Hauber 2020a; Fig. 1). Nests were considered to be active when the clutch size increased on subsequent days, a robin was flushed from the nest, and/or eggs felt warm to touch. Active nests with two or more robin eggs were used for egg deployment experiments.

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Table 1. Experimental studies testing the blunt-pole hypothesis in hosts of avian brood parasites.

Host and parasite species	Host/ parasite egg maculation	Perceivably distinct blunt pole?	Mimetic brood parasite	Experimental treatment (sample size range per treatment)	Statistical support for the blunt-pole hypothesis (odds ratio)	Source
Great reed warbler and common cuckoo	Yes/Yes	Yes	Yes	Painting half of conspecific eggs blue (14-15)	Yes (7.3)	Polačiková & Grim 2010
Great reed warbler and common cuckoo	Yes/Yes	Yes	Yes	Egg shape manipulation to generate blue model eggs with two sharp poles (10), two blunt poles (10), or one of each (10)	Yes (0.43; 9.8; 21)	Zolei et al. 2012
Reed warbler and common cuckoo	Yes/Yes	Yes	Yes	Painting half of conspecific eggs blue (12-13)	Yes (6.75)	Polačiková & Grim 2010
Song thrush and conspecifics	Yes/Yes	Yes	Yes	Painting half of conspecific eggs blue (16-18)	Yes (10.5)	Polačiková & Grim 2010, Polačiková et al. 2010
European blackbird and conspecifics	Yes/Yes	Yes	Yes	Painting half of conspecific eggs blue (15-16)	Yes (6)	Polačiková & Grim 2010
Yellow-bellied prinia and oriental cuckoo	No/No	Yes	Yes	Adding spots to immaculate conspecific eggs (18-22)	Yes (36)	Wang et al. 2020
American robin and brown-headed cowbird	No/Yes	No: for the host Yes: for the parasite	No	Painting half of mimetic model cowbird eggs deep-blue (19) or beige, spotted (11-13)	No (1; 0.37)	Hauber et al. this study

Model eggs were sourced commercially (from www.shapeways.com; "cow bird" egg in versatile natural plastic; for dimension details see Igic et al. 2015); these eggs had been designed to resemble the shape, size, and weight of natural brown-headed cowbird eggs which are smaller than natural robin eggs (Luro et al. 2018). We used three different types of model eggs as control treatments with the paints and/or patterns applied across the full surface of the model egg in triplicate coating (Fig. 1): (I) robin-mimetic blue paint, the resulting paint has a just-noticeable distance (JND) of ~2 JND in avian perceptual space (Hauber et al. 2019); (II) non-mimetic deep-blue paint, with ~19 JND from natural robin egg colours (Hauber et al. 2020b); or (III) a beige paint, with ~5 JND from natural robin egg colours and ~4 JND from natural cowbird eggs (Hauber et al. 2019), with a dark-brown spotting pattern (to resemble the maculation of cowbird eggs). For the robin-mimetic blue, beige, and dark spot colours, we followed the paint-mixing instructions provided in Canniff et al. (2018), whereas the deep-blue paint was an unmixed Ultramarine Series 1 colour; all paints were sourced from the Newton Galeria Acrylic brand (London, UK).

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For the experimental treatments, we painted additional model eggs first with the robin-mimetic blue paint across the full surface (see (I) above), and then we applied a 2 × 2 design (Fig. 1): a) beige-spotted on the sharp pole only (n = 14); b) beige-spotted on blunt pole only (n = 13); c) non-mimetic deep-blue paint on the sharp pole only (n = 20); or d) non-mimetic deep-blue on the blunt pole only (n = 19).

When an active nest was located, it was exposed to one (mode) or more (median: 2) treatments/nest, with one model egg deployed on any given day. We revisited each nest one day after the initial treatment and assessed whether the model egg was present (accepted) or missing (rejected; sensu Abolins-Abols & Hauber 2020b). Any still-present model egg was removed, and we then initiated the next, randomly chosen, different treatment by inserting a new model egg (e.g. Hauber 2020). Adult robins were not captured and individually colour-banded in this study, and so we treated each nest as the sample unit used in statistical analyses. To reduce potential pseudo replication (i.e. studying the same individual female robins across multiple nesting attempts), we conducted these experiments in bouts of 5-7 consecutive days (with the robin incubation period as ~12 days). Thus, we experimented on multiple distinct active nests during each bout of treatments. Additionally, the final sample sizes were lower than those indicated above (Table 2, Table S1), because we excluded all nests lost to predation (some broken or all missing robin eggs) or abandonment (cold and unmoved eggs on two consecutive days), as the latter is not a response to experimental parasitism in American robins (Croston & Hauber 2014).

In our final statistical models (see below), we included both the order of experiment per nest (1st or 2nd) and the number of natural robin eggs in the nest on the day of the experiment, as in some of our earlier research we found the latter metric to impact egg rejection patterns (e.g. Abolins-Abols & Hauber 2020a). We did not include a term of treatment × colour as we did not have an a priori prediction about this interaction.

For statistical analyses, we used a mixed effects logistic regression in the "lme4" package (Bates et al. 2015) of the R Statistical Package (R Core Team 2017). We set the response variable as the bivariate outcome of each trial (outcome: accepted or rejected), with the number of natural robin eggs in the clutch on the day of the experimental trial (eggs), treatment colour (colour: beige-spotted or deep-blue) and pole location of the treatment (treatment: blunt or sharp pole) included as predictor variables and nest ID used as a random effect to accommodate the repeated measures design, while setting α = 0.05, for our data set "pole" [model specifications: glmer (outcome ~ treatment + colour + eggs + order + (1|ID), family = binomial, data = pole)]. We also used Fisher's exact tests to compare whether the one-half painted deep-blue or beige eggs with spots (irrespective of pole location) were rejected at different rates from fully painted eggs of the three different types of controls used in this study.

Table 2. Experimental outcomes in response to model egg types in nests of American robins, with trial outcomes (and %) indicated.

		Host responses	
Colour[a]	Treatment[b]	Accepted	Rejected
Beige-spotted	Blunt Pole	4 (36%)	7 (64%)
	Sharp Pole	2 (15%)	11 (85%)
Deep-blue	Blunt Pole	10 (53%)	9 (47%)
	Sharp Pole	10 (53%)	9 (47%)

[a]Hosts rejected 47% of deep-blue (n = 38) and 75% of beige-spotted (n = 24) model eggs, when combined for whether those colours were on the blunt or sharp poles; z = 2.52, p = 0.01 (with eggs and order as additional predictors and nest ID as a random effect). [b]Hosts rejected 53% of model eggs with treatment colours painted on the blunt poles (n = 30) whereas they rejected 63% of model eggs with colours painted on their sharp poles (n = 32), when combined for whether those were beige-spotted or deep-blue; z = −0.94, p = 0.4 (with eggs and order as additional predictors and nest ID as a random effect).

Results

We found no statistical effects of the number of natural robin eggs in the nest (z = –0.05, p = 1), the order of the experimentation (z = –0.49, p = 0.6), or the location of the pole treatment on rejection rates of model eggs (z = –1.71, p = 0.09), whereas the colour treatment (z = 3.46, p = 0.0005) was a significant predictor, in that beige-spotted eggs were rejected more often than deep-blue eggs (Table 2).

Egg rejection rates of the pole half-painted eggs, relative to fully robin-mimetic blue (control) eggs (10%, n = 10), were higher for both the half-painted beige-spotted model eggs combined (75%, n = 24; Fisher's exact test p = 0.002) and the half-painted deep-blue model eggs combined (47%, n = 38; p = 0.03). In turn, there was no statistical difference between the egg rejection rates of the half-painted

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eggs *vs.* the fully painted (control) eggs of either the beige-spotted (75% *vs.* 88%; n = 24, p = 0.5) or the deep-blue (47% *vs.* 50%; n = 10, p = 1) treatments (Table S1).

Discussion

Although we detected no statistical impact of painting only one-half of the model eggs on the blunt *vs.* the sharp pole, the results indicated a non-significantly higher rejection rate for the sharp *vs.* blunt-painted pole model eggs (Table 2). However, even this trend is in the opposite direction to what had been predicted by the blunt-pole hypothesis and, thus, provides no statistical support for the blunt pole hypothesis (Table 2). Our results also reveal that, in agreement with extensive prior literature (Manna et al. 2017), experimental eggshell colouration and maculation can consistently predict the rejection rates of model eggs, even when they are only painted on half of their surface (Table 2, Table S1). Finally, these statistical outcomes also imply that our sample sizes were sufficient to detect biologically relevant and consistent egg rejection behaviours in the robins within and across experiments (also see Table 1 for sample size comparisons with prior such studies).

Our statistical conclusions concerning the blunt-pole hypothesis are contrary to the findings of prior experimental works on both mimetic, maculated-egg laying hosts of common (Eurasian) cuckoos and on an immaculate egg laying host species of Oriental cuckoos (*Cuculus optatus*; Table 1). These contrasting outcomes, however, are consistent with the suggestion that the comparison of own *vs.* other (parasitic) eggs (e.g. Hauber et al. 2015) may be a critical step in foreign-egg recognition by those host species that are parasitized by mimetic eggs but not by American robins that are parasitized by non-mimetic cowbird eggs (Hauber et al. 2020b).

Specifically, immaculate-egg laying American robins are parasitized by a non-mimetic, maculated-egg laying brood parasite, the brown-headed cowbird (Fig. 1), and so the visual context in this latter host-parasite system is dramatically different from those of the previously studied focal taxa in the context of the blunt pole hypothesis (Table 1). In turn, prior data also demonstrated that self-referent (own *vs.* foreign) egg recognition is not a strong predictor of model egg rejection by American robins (Hauber et al. 2020b). Furthermore, foreign conspecific (robin) eggs are not rejected by adult robins (Luro & Hauber 2017). Therefore, future research regarding pole-specific asymmetric visual information content for egg rejection should be directed towards the species whose eggs the robins reject, namely brown-headed cowbirds. Such an analysis on the relative information-content of cowbird eggs' blunt *vs.* sharp poles using avian-perceivable maculation and spectrometry analyses has not been conducted to-date. However, our preliminary observations of n = 59 eggs from publicly available photographs (from the University of California, Berkeley's Museum of Vertebrate Zoology: e.g. Stoddard et al. 2017, Hauber et al. 2020b) of the *M. ater ater* cowbird subspecies suggested a greater density of spots on the sharp *vs.* the blunt pole of these specimens (t = 1.96, p = 0.052; R.L. Ducay & M.E. Hauber, unpublished data).

Overall, we found no statistical support for the blunt pole hypothesis regarding the direction of asymmetrical information use by this host species in egg rejection decisions in the wild. In turn, we found that robins treat half-painted eggs similarly to fully-painted eggs based on the colour and patterns of the experimental treatment and the resulting appearance. Future work should focus on more species, such as the common redstart (*Phoenicurus phoenicurus*; Rutila et al. 2002, Fossøy et al. 2016, Manna et al. 2020), whose uniformly immaculate eggs themselves are mimicked by immaculate egg laying brood parasite host-races (as seen in the choice of study species by Wang et al. 2020).

Acknowledgements

For access to robin nests, we thank S. Winnicki, F. Hoover, E. Hoover, W. Schelsky and the owners of Wandell's and Country Arbors' Tree Farms and Nurseries. Research for this study was approved by institutional, state and federal agencies. We thank J. Rhodes for assistance with statistical analyses and C. Moskát, H. Pollock, T. Grim, and the editors and referees of this journal for helpful discussions. Funding was provided by the Harley Jones Van Cleave Professorship at the University of Illinois. We are grateful to C. Cicero of the UC Berkeley Museum of Vertebrate Zoology for access to digital cowbird egg specimens. Author contributions: M.E. Hauber conceived the study, M.E. Hauber, J.P. Hoover and D. Hanley designed the experimental treatments, M.E. Hauber, J.P. Hoover and O.R. Rhodes conducted the field experiments, R.L. Ducay conducted the museum data analysis, M.E. Hauber wrote the first draft and all authors edited and approved the submitted versions.

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Supplementary online material

Table S1. Experimental outcomes of model cowbird egg additions to nests of American robins (all from trials in 2020) (https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-1-2021-HauberM.E.-et-al.-Table-S1.docx).

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