

1 **Visual acuity and egg spatial chromatic contrast**
2 **predict egg rejection behavior of American**
3 **robins**

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14 **Keywords:** egg rejection, egg recognition, spatial vision, color vision, brood parasitism

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16 **Summary Statement**

17 We used 3D-printed model eggs with checkered patterns of varying dimensions to test
18 how chromatic visual acuity affects egg recognition in an avian brood parasite host
19 species, the American robin.

20 **Abstract**

21 Color and spatial vision are critical for recognition and discrimination tasks affecting
22 fitness, including finding food and mates and recognizing offspring. For example, as a
23 counter defense to avoid the cost of raising the unrelated offspring of obligate
24 interspecific avian brood parasites, many host species routinely view, recognize, and
25 remove the foreign egg(s) from their nests. Recent research has shown that host
26 species visually attend to both chromatic and spatial pattern features of eggs; yet how
27 hosts simultaneously integrate these features together when recognizing eggs remains
28 an open question. Here, we tested egg rejection responses of American robins (*Turdus*
29 *migratorius*) using a range of 3D-printed model eggs covered with blue and yellow
30 checkered patterns differing in relative square sizes. We predicted that robins would
31 reject a model egg if they could visually resolve the blue and yellow squares as
32 separate features or accept it if the squares blended together and appeared similar in
33 color to the natural blue-green color of robin eggs as perceived by the avian visual
34 system. As predicted, the probability of robins rejecting a model egg increased with
35 greater sizes of its blue and yellow squares. Our results suggest that chromatic visual
36 acuity and viewing distance have the potential to limit the ability of a bird to recognize a
37 foreign egg in its nest, thus providing a limitation to host egg recognition that obligate
38 interspecific avian brood parasites may exploit.

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41 Introduction

42 Animals use spatial chromatic cues when visually detecting predators and prey,
43 choosing mates, and recognizing their own species and close kin (Caves et al., 2018;
44 Cuthill et al., 2017). How animals perceive and discriminate between spatial chromatic
45 visual cues when making decisions relevant to evolutionary fitness is a fundamental
46 question of visual ecology (Cronin et al., 2014; Endler and Mappes, 2017). Behavioral
47 experiments of the perception and discrimination of stimuli that vary both chromatically
48 and spatially have been conducted in a variety of animal taxa, including honeybees *Apis*
49 *mellifera* (Giurfa et al., 1996; Srinivasan and Lehrer, 1988), lizards (Fleishman et al.,
50 2017), and birds (Lind and Kelber, 2011; Potier et al., 2018). In many of these studies,
51 results from a limited number of captive animals subject to extensive training under
52 controlled laboratory settings are considered to be representative and relevant to the
53 model species' natural behaviors and ecologies. Despite the potential for more direct
54 inference of the effect of visual perception and discrimination on fitness in the wild, few
55 studies have tested animals' perception, discrimination, and behavioral responses to
56 ecologically and evolutionarily relevant visual stimuli in their natural environments
57 (Endler and Mappes, 2017).

58 Obligate avian brood parasitism is a rare breeding strategy (~1% of all bird
59 species) in which brood parasites lay their eggs in the nests of different species. In
60 response, potential hosts either recognize and reject the foreign egg(s) and/or
61 nestling(s) or raise the parasitic offspring at a cost to their own fitness (Davies, 2000).
62 Visually discriminating own vs. parasitic eggs can be an exceptionally challenging task
63 when brood parasites produce highly mimetic eggs (Stoddard and Hauber, 2017). As a
64 result, hosts may commit recognition errors and mistakenly reject their own eggs,
65 rendering egg rejection a risky defense strategy with potentially severe consequences
66 to host fitness (Davies et al., 1996; Lotem et al., 1995).

67 Arguably, avian brood parasitism research to test how birds recognize eggs is at
68 the forefront avian visual perception and discrimination experiments conducted in the
69 wild (Stoddard and Hauber, 2017). Model plaster (Davies and Brooke, 1989; Honza et
70 al., 2007; Rothstein, 1982) or 3D printed eggs (Igic et al., 2015) can be systematically

71 painted with ranges of natural avian colors (Canniff et al., 2018; Hauber et al., 2015)
72 and spotting patterns (Dainson et al., 2017; Hanley et al., 2019; Luro et al., 2018) and
73 placed into host species' nests to test if the attending parents discriminate and
74 recognize the model eggs by touching them (Soler et al., 2017), setting them aside
75 within the nest, or removing them from the nest. Recent work combining visual modeling
76 (Vorobyev and Osorio, 1998) with foreign-egg rejection experiments has demonstrated
77 that 1) birds have a perceptual bias towards responding to natural blue-white-brown egg
78 color gradients (Abolins-Abols et al., 2019; Manna et al., 2020), but do not respond
79 predictably to purple-green color gradients not found among natural eggs (Hanley et al.,
80 2017); 2) egg background color and egg spotting presence (and/or color) combine
81 together as a multicomponent cue and can greatly increase or decrease egg rejection
82 responses, depending on the host species' own egg appearance (Dainson et al., 2017;
83 Hanley et al., 2019; Luro et al., 2018); and 3) host species may use achromatic
84 patterning and spatial features such as egg spotting and scrawling when recognizing
85 and rejecting foreign eggs (Spottiswoode and Stevens, 2010; Stoddard et al., 2014).
86 Egg rejection experiments require neither captivity nor extensive training and allow for
87 individually repeated and/or population-wide tests of avian visual discrimination
88 capabilities in an ecologically relevant context.

89 Despite great advances in our knowledge of how birds recognize foreign eggs
90 within their nests using visual cues including egg size, shape, color and spotting, no
91 study to date has examined whether egg spatial and chromatic features may be
92 simultaneously integrated by the host's visual system to influence egg recognition. For
93 instance, how well can birds resolve details of egg spotting pattern and color when
94 viewing eggs from various distances? Do some egg spotting patterns blend in with each
95 other and with the egg background from the bird's point of view? Here, we tested if and
96 how American robins *Turdus migratorius* (hereafter: robins), a robust rejecter of
97 parasitic brown-headed cowbird *Molothrus ater* eggs (Rothstein, 1982), respond to
98 differences in spatial chromatic contrast when viewing and deciding to accept or reject a
99 foreign egg. The underlying assumption is that visual acuity (i.e., visual spatial
100 resolution) can limit the ability of birds to resolve details in the chromatic spatial pattern
101 of eggs, as has been found in diverse taxa under different ecological conditions (Caves

102 et al., 2018). We used avian visual modelling and visual acuity estimates for lateral and
103 binocular vision of American robins to create model eggs with spatial chromatic patterns
104 along a gradient of increasing difficulty for robins to visually resolve the patterned eggs
105 as different from natural robin eggs. To this end, we i) designed a range of 3D printed
106 model eggs and covered them with a suite of novel, blue and yellow checkered
107 patterns, where both colors were present in equal proportions but differed in their
108 relative inter-square distances to one another across model eggs, and ii) estimated a
109 spatial chromatic discrimination threshold distance at which the blue and yellow squares
110 should blend from the robin's visual perspective and appear similar to the natural robin
111 egg's immaculate blue-green coloration. We predicted that robins would reject the
112 model egg when they could resolve the blue and yellow squares as separate features,
113 but would accept the artificial egg when they could not resolve the squares apart (i.e., if
114 the blended color of blue and yellow squares appeared similar to the blue-green color of
115 natural robin eggs).

116

117 **Methods**

118 *Experimental Egg Pattern Design*

119 We generated test checkerboard patterns of various combinations of blue and
120 yellow colored squares, whose centers were spaced 0.15 mm apart from one another
121 and printed the test color patterns on transferrable decal paper (Sunnyscopa Film-Free
122 Waterslide Decal Paper Multi Use 8.5x10in [216x254mm], Sunnyscopa, South Korea)
123 using an HP Color LaserJet Pro MFP M281fdw with HP202A black, yellow, cyan and
124 magenta toners (HP Development Company, L.P. USA). Our printer had a color printing
125 resolution of up to 600 x 600 dpi, and we printed patterns at 300 dpi resolution in tagged
126 image file format (TIFF). We took spectral reflectance measurements of the printed test
127 color patterns using an Ocean Optics JAZ spectrometer (Ocean Optics, Inc. USA) with
128 a 400 μ m fiber optic cable and a reflectance probe fitted with a black rubber cap to block
129 external light. We measured a 12.57 mm² circular area of the pattern from a 10 mm
130 distance at 90° angle. The reflectance probe had an acceptance angle of 24.8°, and
131 therefore the reflectance measurements were of both blue and yellow colors together

132 (using Eqn 1.0, $24.8^\circ > 0.015^\circ$ angle of single 0.150mm blue or yellow square
133 measured from 10mm away).

134 *Eqn 1.0* (Swearer, 2011)

$$\text{Visual Angle } \theta = 2 \cdot \text{atan}\left(\frac{\text{Object Size}}{2 \cdot \text{Object Distance}}\right)$$

136 We used a receptor-noise limited model (Vorobyev and Osorio, 1998) to
137 calculate avian-perceived chromatic and achromatic Just Noticeable Differences (JNDs)
138 between our “blended” test blue and yellow pattern, the blue color alone, the yellow
139 color alone, and a range of $N = 22$ natural robin eggs, using reflectance spectra data
140 from Croston and Hauber (2015a) to determine the best printed blue/yellow combination
141 for mimicking natural robin egg colors (Fig. 1). We used peak sensitivities of UVS, SWS,
142 MWS and LWS cone photoreceptors, cut-off wavelengths (λ_{cut}) for photoreceptors’
143 respective oil droplets, relative photoreceptor densities, and ocular media transmittance
144 of the congeneric common (European) blackbird *Turdus merula* (Hart et al., 2000). The
145 model assumed robins viewed the eggs under bright daylight conditions (D65 irradiance
146 spectrum from Maia et al., 2019), eggs were viewed against the background of a typical
147 dry brown grass lining in natural robin nests (nest reflectance data were sourced from
148 Aidala et al., 2015), and a Weber fraction value of 0.1 for calculating photoreceptor
149 noise values (Olsson et al., 2018).

150 Previous work has shown that visual modelling of chromatic perceptual
151 differences (i.e., JNDs) using the receptor-noise limited model (Vorobyev and Osorio,
152 1998) can reliably predict the likelihood of a host recognizing and rejecting a foreign egg
153 (Avilés et al., 2010; Cassey et al., 2008; Honza and Cherry, 2017). Therefore, we chose
154 a “blended” blue/yellow (blue R,G,B = 45, 169, 239; yellow R,G,B = 246, 236, 112) color
155 combination with the lowest median chromatic JND value and range from natural robin
156 eggs (median = 2.51 JND and range = 1.26 to 4.65 JND, Fig. 1). Both achromatic and
157 chromatic JNDs of model egg colors are listed in Figure 1C. Because JND values close
158 to 1 are expected to be more difficult to discriminate between than JND values much

159 greater than 1 (Vorobyev and Osorio, 1998), we predicted robins would perceive our
160 blended blue-yellow model egg as quite similar to natural robin eggs, but not as entirely
161 indistinguishable from them (i.e., imperfectly mimetic). All avian visual modeling was
162 done using the *pavo* v2.3 package (Maia et al., 2019) in *R* v 3.6.1 (R Core Team, 2017).

163 The ability to spatially resolve visual stimuli varies across the avian retina
164 (Fernández-Juricic, 2012). Many bird species, like the American robin, tend to have a
165 center of acuity vision (i.e., fovea) with high spatial resolution ability, surrounded by
166 peripheral retinal area with much lower spatial resolution ability (Moore et al., 2017). In
167 the American robin, the fovea projects into the lateral visual field, whereas portions of
168 the retinal periphery project into the binocular field (PB and EF-J, unpublished data).
169 Peak visual acuity of the robins is estimated to be 14.54 cycles/degree for lateral
170 (foveal) vision and 8.75 cycles/degree for binocular vision (peripheral to the fovea)
171 (using retinal ganglion cell counts and eye axial diameter; PB and EF-J, unpublished
172 data). We used the minimum angle of resolution calculated from robin peak foveal

173 visual acuity (minimum angle of resolution = $0.069^\circ = \frac{1}{14.54 \text{ CPD}}$) to generate a range of
174 11 checkered square patterned eggs with visual angles spanning both above and below
175 the minimum angle of resolution at various probable viewing distances (1 to 30cm, Fig.
176 2A). All visual angles were calculated using Eqn 1.0, where object size is the inter-
177 square distances of the checkered patterns and object distance ranged between 1-30
178 cm. Viewing distances were roughly estimated as the distance from a robin's eye, while
179 the robin views an egg using both lateral and binocular vision, to the surface of the
180 model egg using video data of robins viewing eggs from (Hauber et al., 2019) (e.g., see
181 <https://youtu.be/GBTML1zccQA>) (Fig. 2A). Checkered pattern designs were all 6 cm x 6
182 cm in total area and inter-square distances were 0.150 mm, 0.199 mm, 0.299 mm,
183 0.397 mm, 0.594 mm, 0.845 mm, 0.982 mm, 1.177 mm, 1.463 mm, 1.936 mm, and 2.40
184 mm. We also created a "control" 0.0 mm pattern using a checkered pattern with 0.150
185 mm inter-square distances and the Gaussian Blur filter in ImageJ (Schneider et al.,
186 2012) to blend the blue and yellow squares together and create a uniform blue-green
187 colored stimulus (intended to mimic natural robin egg color).

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190 *Artificial Egg Design*

191 We used 3D printed, brown-headed cowbird-sized model eggs (2.25cm length x
192 1.69 cm width in size, “Cowbird egg smooth”, purchased from Shapeways, Inc.,
193 following Igic et al., 2015) for all experimental model eggs. Cowbird-sized eggs have
194 been used in previous experiments and can be successfully grasped and removed from
195 nests by adult robins (Luro and Hauber, 2017). Experimental egg pattern designs were
196 printed as 6 cm x 6 cm squares onto transferrable decal paper (see *Experimental Egg*
197 *Pattern Design* above). We cut out, wrapped, and glued the decal patterns onto the
198 model eggs in a vertical orientation towards the egg poles and used small curved
199 scissors to trim away excess decal. Air bubbles were removed by gently pressing the
200 decals by hand until the pattern was flush and smooth on the surface of the model egg.
201 Eggs were left to dry for at least 48 hours before being placed into wild robins’ nests in
202 the field.

203 *Egg rejection experiments*

204 We searched for active robin nests in Champaign County, Illinois, USA, during
205 May through June of 2019. Upon finding a nest with at least two eggs, we recorded the
206 current clutch size, added a randomly chosen model egg into the nest, and monitored
207 the nest daily until the artificial egg went missing from the nest (rejected) or up to 3 days
208 from egg insertion if the egg remained in the nest (accepted; sensu Luro and Hauber
209 2017). Adult robins were not captured or marked for this study but we visited three
210 distant sites (more than 5 km apart), used multiple simultaneously active nests within
211 each site, and tested each nest once with a single model egg treatment to reduce
212 biological non-independence. Nest abandonment is not a response to experimental
213 parasitism in robins (Croston and Hauber, 2014), and so data from abandoned (n = 4)
214 or depredated nests (n = 2; out of 33 total nests tested) were not included in the
215 analyses. Sample sizes for each treatment were as follows: control pattern, N = 2; 0.150
216 mm, N = 2; 0.199 mm, N = 1; 0.299 mm, N = 2; 0.397 mm, N = 3; 0.594 mm, N = 2;

217 0.845 mm, N = 1; 0.984 mm, N = 2; 1.177 mm, N = 3; 1.463 mm, N = 2; 1.936 mm, N =
218 2; and 2.40 mm, N = 5.

219

220 *Statistical Modelling*

221 We used the *brms* package (Bürkner, 2017) in *R* v3.6.1 (R Core Team, 2017) to
222 run logistic regression models predicting robins' rejection/acceptance responses to
223 checkered model eggs placed into their nests. Our full model's predictors included the
224 inter-square distance (mm) of the model egg, the nest clutch size when we inserted the
225 model egg into the nest, and the date at which the experiment was initiated. Our
226 reduced models included the inter-square distance (mm) of the model egg, and either
227 clutch size or date of the experiment. The simplest model included the inter-square
228 distance (mm) of the model egg as the only predictor of robins' egg rejection responses.
229 We included weakly informative priors (Gelman et al., 2017) for the model intercepts
230 (Student T: df = 3, location = 0, scale = 5) and predictors (Student T: df = 3, location = 0,
231 scale = 5). We ran each model for 10,000 iterations across 4 chains and assessed
232 Markov Chain Monte Carlo (MCMC) convergence using the Gelman-Rubin diagnostic
233 (Rhat) (Gelman et al., 2013). Finally, we used leave-one-out cross validation (LOO) to
234 compare models and determined relative model accuracies for predicting robins' egg
235 rejection responses using the expected log pointwise predictive density (ELPD)
236 differences between models (Vehtari et al., 2017). The most accurate model is ranked
237 as ELPD = 0 and all other model ELPD values are relative to the best model's ELPD.

238 Finally, we determined the approximate inter-square distance rejection threshold
239 (inter-square distance at which rejection probability is 0.5) by simulating posterior fitted
240 values from the most accurate model for experimental egg inter-square distances
241 between 0-2.4mm at 0.001mm increments and calculating the posterior median and
242 75% credible interval of inter-square distance for posterior fits with rejection probability =
243 0.5. We used 50% as our arbitrary rejection threshold because the median clutch size
244 for robins nests of our experiments was 3—therefore if robins were only responding to
245 the addition of an egg into their nests and randomly guessing which egg to reject, they
246 would correctly reject our model egg approximately 25% of the time. Thus, using a 0.5

247 probability of egg rejection as a threshold omits the possibility of random guessing while
248 also selecting for a model egg pattern that is not readily discriminated and rejected (i.e.,
249 > 0.5 probability of rejection).

250 **Table 1 Comparisons of models predicting American robins' responses to blue-yellow checkered**
251 **artificial eggs.** Models are ordered by their prediction accuracy from leave-one-out cross validation: the
252 top model has an expected log pointwise predictive density (ELPD) difference of 0, and all other models
253 have negative ELPD difference values.

Model Predictors	ELPD Difference \pm SE
<i>Inter-Square Difference (mm)</i>	0
<i>Inter-Square Difference (mm) + Clutch Size</i>	-1.12 \pm 0.55
<i>Inter-Square Difference (mm) + Date</i>	-1.22 \pm 0.37
<i>Inter-Square Difference (mm) + Clutch Size + Date</i>	-2.59 \pm 0.7

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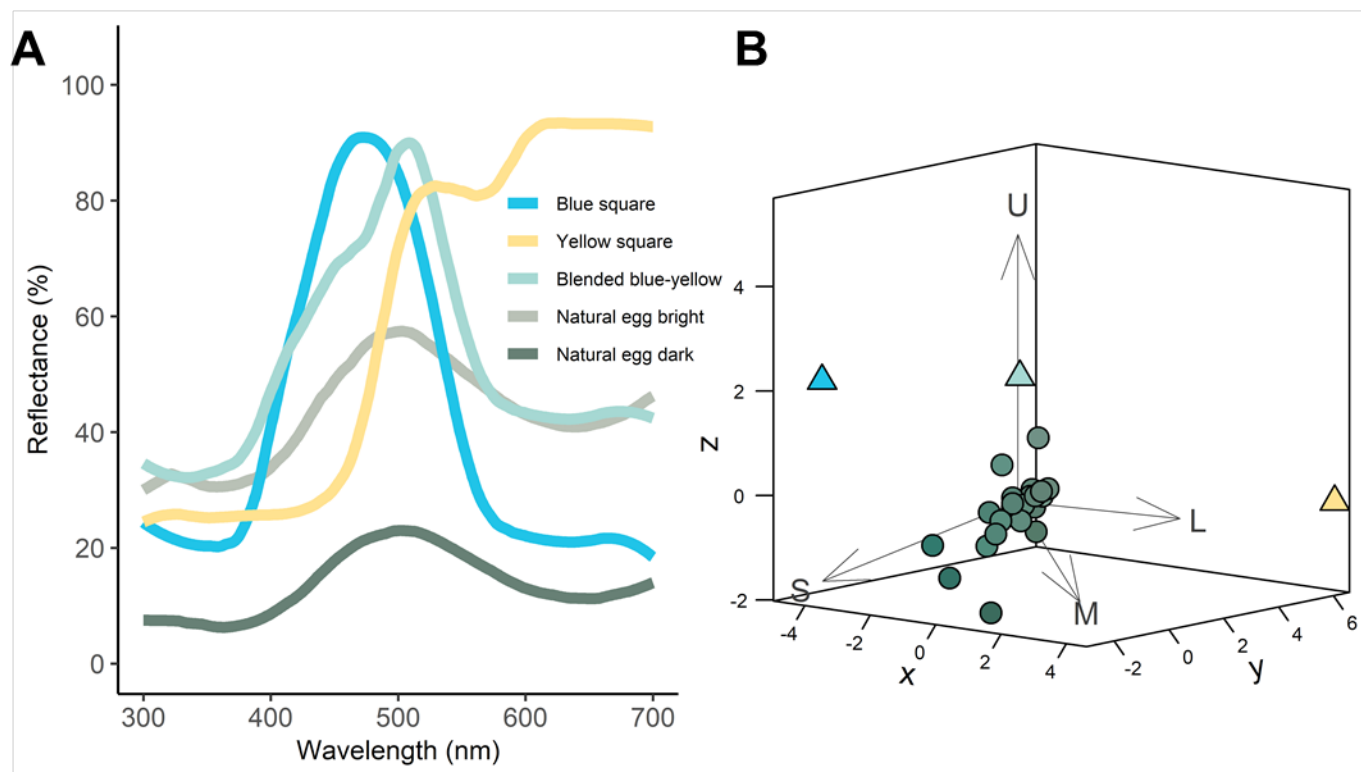
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260 **Figure 1. Avian visual modeling of experimental egg colors.** **A** Representative reflectance spectra of
 261 blue square, yellow square, blended blue-yellow checkered pattern and two natural robin eggs. **B** 3D
 262 Euclidian distance Just Noticeable Difference (JND) plot of blue square (triangle), yellow square (triangle),
 263 blended blue-yellow checker pattern (triangle) and N=22 natural robin eggs (circles). Relative distance of
 264 points to each other are in units of JNDs, arrows represent each avian cone photoreceptor type: *U* =
 265 ultraviolet-sensitive cone, *S* = shortwave-sensitive cone, *M* = mediumwave-sensitive cone, *L* = longwave-
 266 sensitive cone. Natural robin egg reflectance spectra on the **A** were used from English and Montgomerie
 267 (2011) for “bright” and “dark” representative robin egg reflectance spectra, and robin egg reflectance
 268 spectra from Croston and Hauber, 2015b were used for **B** and **C** the calculation of JND values.

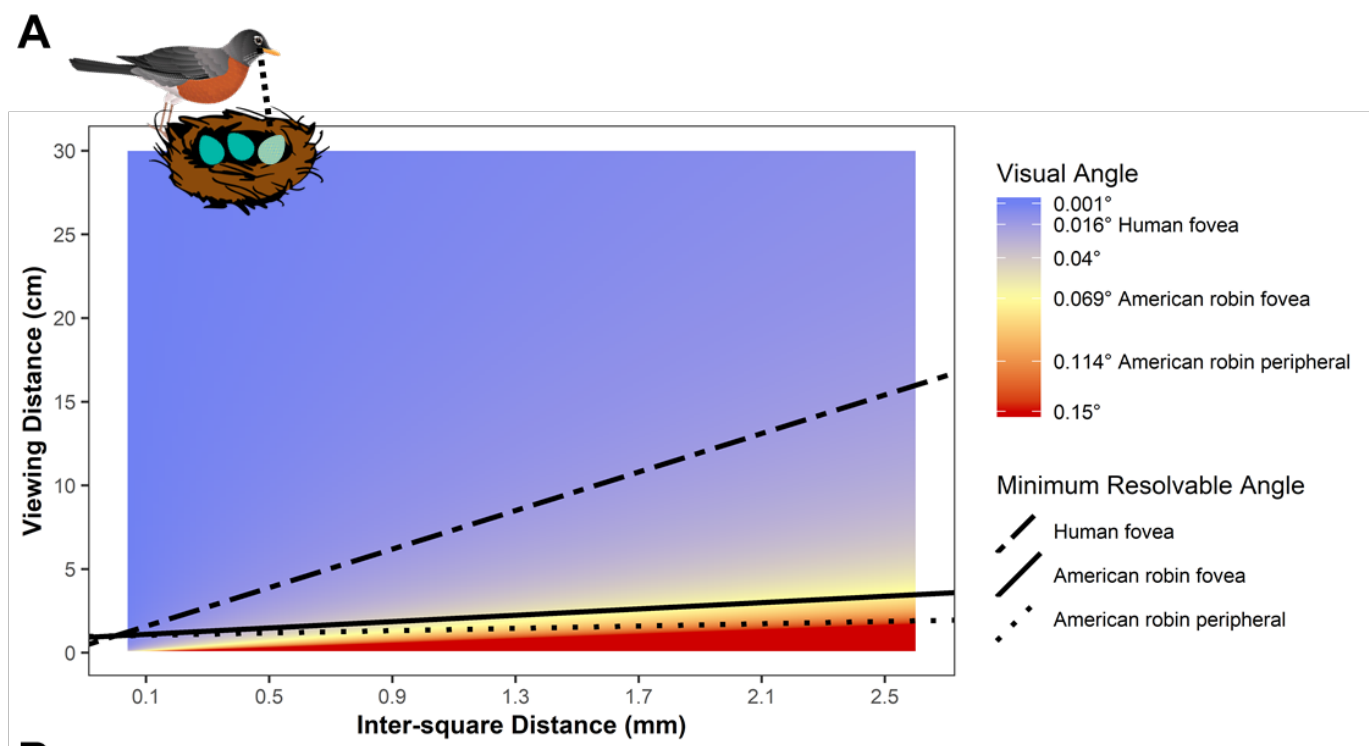


C

Stimulus	Chromatic JND from natural robin eggs median (range)	Achromatic JND from natural robin eggs median (range)
<i>Blended blue-yellow</i>	2.5 (1.3, 4.6)	11.7 (7.9, 17)
<i>Blue square</i>	5.3 (4.2, 5.9)	8.7 (4.8, 13.9)
<i>Yellow square</i>	7.8 (7, 10.2)	14.5 (10.7, 19.8)
Blue vs. Yellow square		Chromatic JND = 12.5 Achromatic JND = 5.9

270 **Figure 2. Visual angles of model eggs** from the human perspective (dot-dashed line, 60 cycles/degree
 271 acuity), and from the American robin's (*Turdus migratorius*) perspective using either lateral (foveal acuity,
 272 14.54 cycles/degree) or binocular (peripheral acuity, 8.75 cycles/degree) vision. Visual angles were
 273 calculated from modelled pattern inter-square distances and viewing distances using *Eqn. 1.0*. We
 274 predicted model egg color should appear similar to natural robin egg color when the robin's visual angle is
 275 below the foveal and/or peripheral minimum resolvable angles as visual angles lower than the minimum
 276 resolvable angle should cause image blending of blue and yellow squares from the robin's perspective.
 277 Acuity-corrected images were modeled using *AcuityView* image transformations (Caves and Johnsen,
 278 2017) in *ImageJ* (van den Berg et al., 2020).

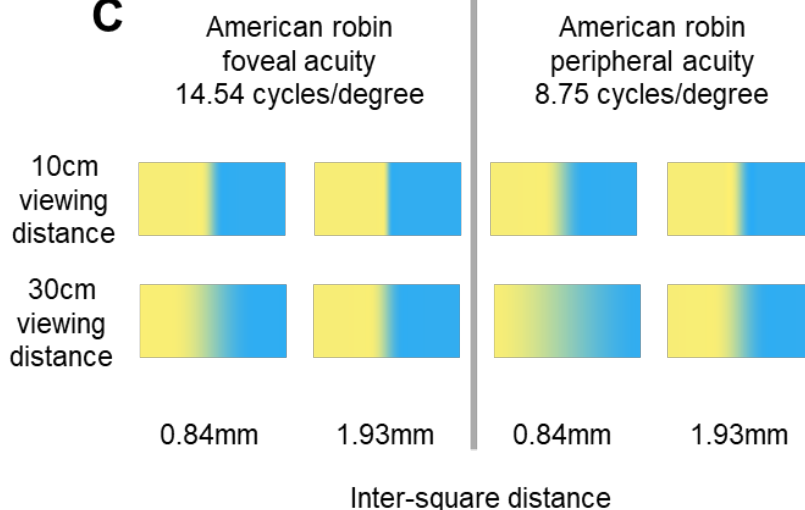
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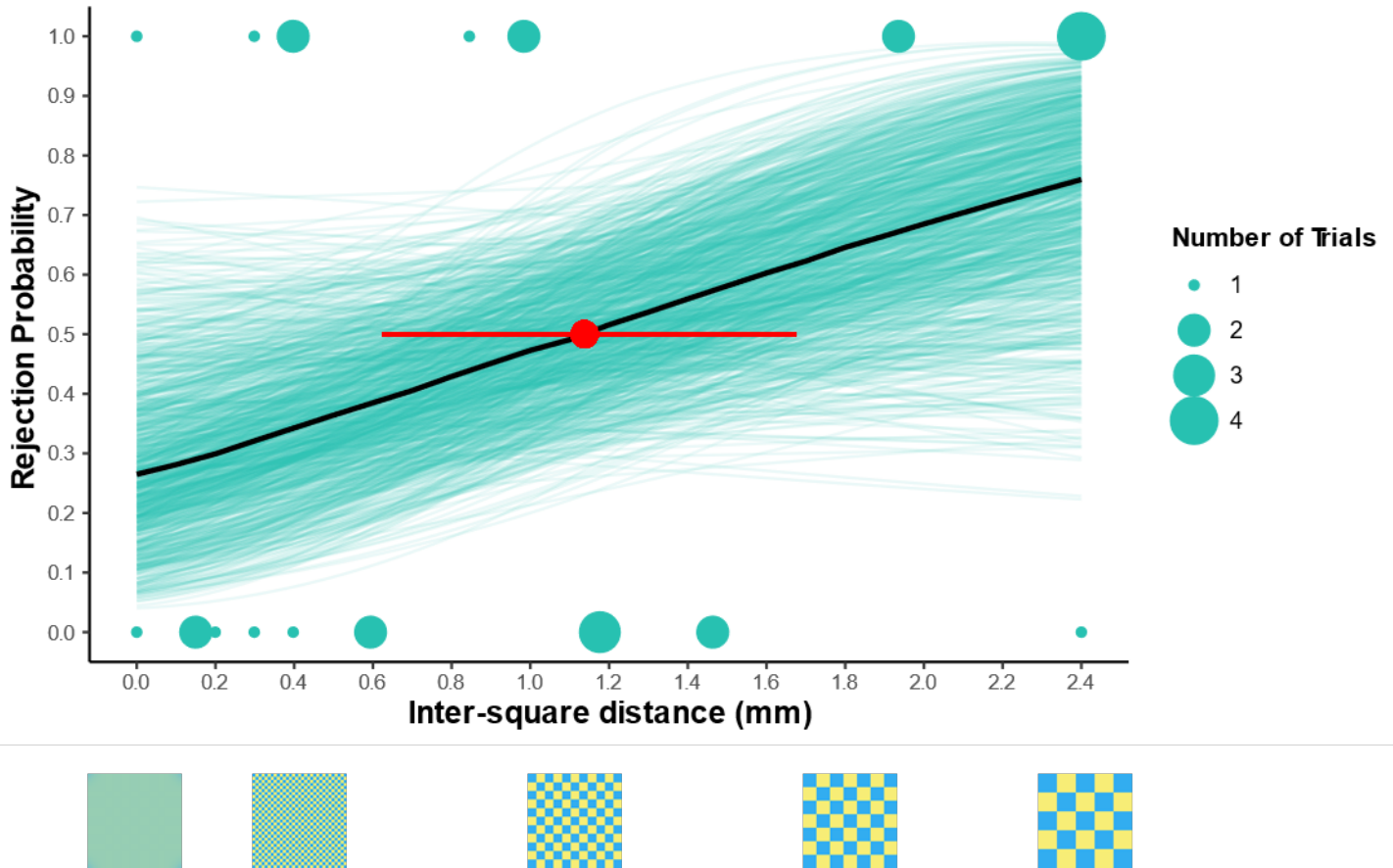
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281 **Figure 3. Model-fitted probabilities of American robin egg rejection responses to blue-yellow**
282 **checkered model eggs.** Blue-green lines are simulated model fits for $N = 1000$ posterior draws; black
283 line is the median of all posterior draws. Model egg inter-square distance between blue and yellow
284 squares at which robins are predicted to reject model eggs at a 0.5 probability is indicated by red 75%
285 credible interval and posterior median. Inter-square distances of several representative checkered pattern
286 images are true to the scale of the x-axis.

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294 Results

295 We used data on the outcomes of the egg rejection experiments at $N = 27$
296 different nests with a median of $N = 2$ experimental replicates per model egg type for all
297 11 different checkered model egg treatments and the control model egg (0.0 mm inter-
298 square distance). We obtained ≥ 10000 effective samples for each model parameter
299 and all models' Markov Chains (MCMC) successfully converged (Rhat = 1 for all
300 models' parameters). American robins' egg rejection responses were best predicted by
301 a model with egg inter-square distances (mm) as the only predictor (Table 1; ELPD
302 difference = 0). However, there was also fair amount of uncertainty in the model's
303 predictive reliability (posterior median Bayes $R^2 \pm$ median absolute deviation [95%
304 credible interval] = 0.108 ± 0.095 [0.001, 0.272]; where Bayes R^2 is the model predicted
305 variance divided by the sum of model predicted variance and model error variance, see
306 Gelman et al., 2019). Robins' egg rejection responses increased with larger model egg
307 blue-yellow inter-square distances (mm) (posterior median \pm median absolute deviation
308 [95% highest-density interval] = 0.89 ± 0.53 [-0.17, 1.97]) (Fig. 3). Finally, we found that
309 the approximate 50% egg rejection threshold for robins' responses to the blue-yellow
310 checkered model eggs was 1.138mm, corresponding to a visual angle range of 0.114°
311 to 0.0114° from viewing distances of 1 cm and 10 cm respectively, with this
312 approximation having a wide range of credible values (approximate 50% threshold
313 posterior median [75% credible interval] = 1.138 mm [0.623 mm, 1.675 mm]). Given a
314 50% egg rejection threshold pattern inter-square distance of 1.138mm, the pattern
315 should begin to blend from the robin visual perspective using either lateral (foveal) or
316 binocular (peripheral) vision at viewing distances > 3 cm.

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322 Discussion

323 Our results suggest that American robins respond predictably to spatial
324 chromatic contrasts when rejecting a foreign egg from the nest. Egg rejection responses
325 were best predicted by inter-square distances of the blue-yellow checkered patterns of
326 model eggs alone (Table 1), as robins were more likely to reject model eggs with larger
327 inter-square distances (Fig. 3). These findings are consistent with the prediction that the
328 combination of blue and yellow colored squares of our model eggs likely appears similar
329 to natural blue-green robin eggs from the robin's perspective when robins are unable to
330 completely resolve the colored squares as separate features (i.e., when the robin's
331 visual angle is below the minimum resolvable angle, Fig. 2).

332 Most passerine birds, including American robins, have laterally placed eyes and
333 often move both their eyes and head when viewing an object of interest to align their
334 high-acuity foveal vision, or align their eyes to gaze at an object using binocular vision
335 with lower acuity perifoveal retinal regions of the eyes (Land, 2014; Moore et al., 2017).
336 The distance at which robins view eggs in the nest, along with their visual acuity when
337 viewing eggs with lateral (foveal) or binocular (peripheral) vision, is equally important for
338 putting our results into context. For instance, if robins consistently inspect their eggs
339 using either lateral or binocular vision from distances > 3 cm, then it is very likely that
340 robins only partially resolved the blue and yellow squares as separate features for all
341 our experimental model eggs (Fig. 2, both foveal and peripheral minimum resolvable
342 angle lines for the American robin). Other factors expected to affect the ability of robins
343 to resolve spatial chromatic contrasts of our model eggs include: pupil size,
344 photoreceptor arrangement and spacing, and potential variation in the spectral profile of
345 light illuminating the eggs and nest (Cronin et al., 2014; Land et al., 2012).
346 Characterizing these visual properties in American robins would make it possible to
347 more precisely test and model robin visual discrimination of egg features. However,
348 visual physiology alone, i.e., modeling visual perception using ocular anatomy and
349 retinal physiology, cannot wholly predict egg recognition and egg rejection behavior of
350 avian brood parasite hosts (Croston and Hauber, 2014; Hanley et al., 2017; Manna et
351 al., 2017; Stoddard and Stevens, 2011). Upon gathering visual information, brood

352 parasite hosts likely use a combination of cognitive decision rules when recognizing and
353 deciding to reject a foreign egg, including counting eggs in the nest (Lyon, 2003),
354 rejecting the most dissimilar egg amongst all eggs in the nest (Moskát et al., 2010), and
355 comparing a foreign egg's appearance against an internal representation of own eggs'
356 appearance(Stevens et al., 2013).

357 Our study also demonstrates the utility of avian egg recognition experiments
358 using model eggs for testing mechanisms fundamental to visually-guided behaviors.
359 Critically, the egg rejection behavior analyzed here is a fitness-relevant behavior for
360 American robins because a small minority of robins do accept brown-headed cowbirds
361 eggs laid in their nests (Lowther, 1981), and raising parasitic cowbird nestlings reduces
362 the fledging success of robin nestlings (Croston and Hauber, 2015a). Surprisingly, many
363 host species that are frequently parasitized by avian brood parasites do not reject
364 foreign eggs laid into their nests even when there is a significant fitness cost to raising
365 unrelated brood parasitic nestlings (Medina and Langmore, 2016). Our results
366 demonstrate that host visual acuity and egg viewing behavior has the potential to limit
367 the ability to detect and discriminate between spatial and chromatic features of eggs.
368 Specifically, hosts can gather more detailed and accurate visual information about egg
369 coloration and patterning by viewing eggs in their nest more often with their high acuity
370 foveal vision and/or viewing eggs from shorter distances to increase the visual angles of
371 the eggs' patterning. For example, common cuckoos (*Cuculus canorus*) have evolved
372 better egg color and pattern mimicry for host species that have robust egg rejection
373 defenses (Stoddard and Stevens, 2010; Stoddard and Stevens, 2011). Perhaps cuckoo
374 hosts that are skillful egg rejecters have also evolved egg viewing behaviors to better
375 resolve the chromatic and spatial patterning of eggs in their nest, whereas species
376 exhibiting weaker egg rejection responses to foreign eggs have not. Importantly, future
377 experimental studies directly linking predictions derived from visual modelling with
378 behaviors that have known fitness consequences will greatly advance the field of visual
379 ecology (Luro and Hauber, 2020).

380 Overall, our combined modelling and experimentation revealed that American
381 robin acuity can predict egg rejection responses to foreign eggs, and spatial chromatic

382 contrasts of eggs may be an important visual cue used by birds when viewing and
383 recognizing eggs in their nests. The implication is that visual acuity can impose limits on
384 egg recognition ability in hosts, an important task with considerable evolutionary fitness
385 consequences for hosts of avian brood parasites. Specifically, resolving power
386 constraints of the hosts could be exploited by brood parasites to minimize host detection
387 of parasitic eggs. Finally, failing to recognize differences in visual perception between
388 ourselves and non-human animals is notoriously common and problematic in
389 comparative visual perception studies (Caves et al., 2019). Comprehending differences
390 in visual acuities between ourselves and other species may be especially difficult,
391 considering humans have relatively high visual acuity (Caves et al., 2018). Thus, our
392 results provide a compelling example of how our own biases in the detection, perception
393 and/or processing of visual information may be vastly different from those of birds.

394 **Ethics Statement**

395 All experimental methods were reviewed and approved by the Institutional Animal care
396 and Use Committee (IACUC) at the University of Illinois (# 17049). Field work was
397 approved by the USA Fish and Wildlife Service (# MB08861A-3) and by the Illinois
398 Department of Natural Resources (NH19.6279).

399 **Declaration of Interest**

400 All authors declare they have no conflicts of interest associated with this study.

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408

409 **Author Contributions**

410 **Alec Luro:** Conceptualization, Methodology, Software, Formal Analysis, Data Curation,
411 Visualization, Writing-Original Draft. **Patrice Baumhardt:** Methodology, Writing-Review
412 & Editing. **Esteban Fernandez-Juricic:** Methodology, Writing-Review & Editing,
413 Supervision. **Mark Hauber:** Conceptualization, Methodology, Investigation, Resources,
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