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Variation in multicomponent recognition cues alters egg rejection decisions: a test of the optimal acceptance threshold hypothesis

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The optimal acceptance threshold hypothesis provides a general predictive framework for testing behavioural responses to discrimination challenges. Decision-makers should respond to a stimulus when the perceived difference between that stimulus and a comparison template surpasses an acceptance threshold. We tested how individual components of a relevant recognition cue (experimental eggs) contributed to behavioural responses of chalk-browed mockingbirds, *Mimus saturninus*, a frequent host of the parasitic shiny cowbird, *Molothrus bonariensis*. To do this, we recorded responses to eggs that varied with respect to two components: colour, ranging from bluer to browner than the hosts' own eggs, and spotting, either spotted like their own or unspotted. Although tests of this hypothesis typically assume that decisions are based on perceived colour dissimilarity between own and foreign eggs, we found that decisions were biased toward rejecting browner eggs. However, as predicted, hosts tolerated spotted eggs more than unspotted eggs, irrespective of colour. These results uncover how a single component of a multicomponent cue can shift a host's discrimination threshold and illustrate how the optimal acceptance threshold hypothesis can be used as a framework to quantify the direction and amount of the shift (in avian perceptual units) of the response curve across relevant phenotypic ranges.

This article is part of the theme issue 'The coevolutionary biology of brood parasitism: from mechanism to pattern'.

1. Introduction

Decision-making is critical for survival and reproduction [1], but animals often face challenging decisions involving discriminating between novel stimuli in a variety of contexts. Thus, the ability to produce flexible responses to novel situations is necessary for adaptive decisions [2]. One approach for making decisions between stimuli is to set a (flexible) threshold based on the similarity of the traits of each stimulus, such that differences greater than a threshold elicit a response. This 'optimal acceptance threshold hypothesis' was proposed almost 30 years ago [2] and has been used to predict decisions across a range of contexts: pollination [3], same-sex partnership [4], social insect nest-mate recognition [5] and foreign egg rejection [6]. In each case, stimuli vary and

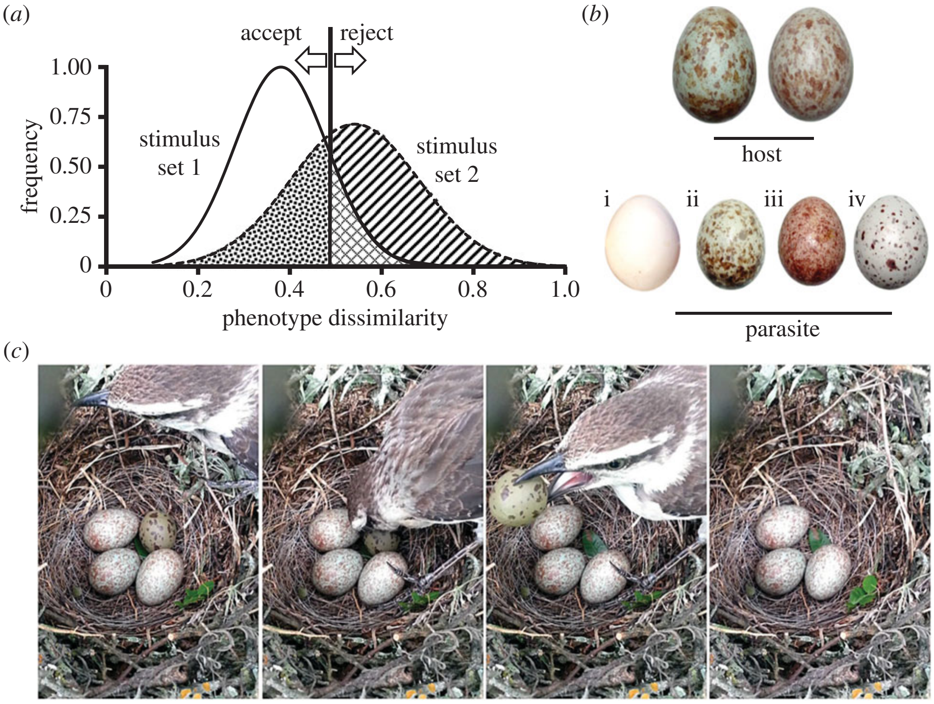

Figure 1. The optimal acceptance threshold hypothesis is a theoretical model used to understand the outcomes of discrimination decisions between (*a*) stimuli that vary relative to a template, e.g. in making decision between potential non-self and self (modified from [2]). Hosts of avian brood parasites can compare their own eggs (or an internal template of their eggs) with other eggs in their nests. When the difference between the template and the focal stimulus is greater than the acceptance threshold (solid vertical line), the theory predicts rejection by the host, but hosts should accept the stimulus when the difference is less than the threshold. Here we illustrate two sets of stimuli, such that stimulus set 1 represent eggs that should not be rejected (e.g. last laid eggs that appear different) and stimulus set 2 represents eggs that should be rejected (e.g. a parasite's egg). Thus, dotted areas represent acceptance errors, the crosshatched area represents rejection errors, and the linear hatched area represents correct rejection decisions. The chalk-browed mockingbird has a (*b*) blue–green spotted egg and is parasitized by the shiny cowbird, which has polymorphic eggs that vary in coloration and spotting (eggs i–iv). Mockingbirds tend to reject pure white, unspotted, cowbird eggs (i), while they accept other cowbird colour morphs: blue–green (ii) and both heavily and lightly spotted white eggs (iii and iv, respectively). However, the presence of spots may be sufficient to 'shift' an egg from the 'reject' to the 'accept' side of the acceptance threshold, because an additional matching feature would increase the uncertainty of the decision. This host rejects eggs through (*c*) grasp rejection, which we illustrate through a series of images showing a host returning to its nest, examining the egg, grabbing the egg and removing it (left to right). Photo credit: A. V. López.

the optimal choice is context dependent, i.e. an acceptable choice in one situation would not necessarily be an adaptive decision in another (figure 1*a*).

The optimal acceptance threshold hypothesis has found substantial traction within studies of avian brood parasitism. In such systems, brood parasites lay their eggs in hosts' nests, imposing the cost of parental care upon foster parents [7–9]. A host's ability to discriminate between its own and the parasite's egg, and appropriately respond to it, is an important evolved host defence against brood parasitism [7,8]. Hosts may respond to the presence of a brood parasite's egg in their nest by deserting the clutch, by burying the parasitic egg, or by ejecting it from the nest [10,11]. When making these decisions, hosts must balance the risk of accepting a parasitic egg (acceptance error) or mistakenly rejecting one of their own (rejection error).

Avian eggshell coloration and patterning can provide salient information for hosts to make rejection decisions [8]. Owing to the limited pigmentary basis for colour production in avian eggshells [12,13], the coloration of birds' eggs is constrained to fall along a gradient ranging from blue–green to brown within the avian perceptual colour space [14,15]. Most applications of the optimal acceptance threshold hypothesis to brood parasitism have assumed hosts base their decisions on absolute perceivable differences between their own eggs (or a template of them) and the foreign egg(s) in the nest [16]. This implies that hosts set thresholds along phenotypic extrema on each side of a phenotypic range ('multiple thresholds'), in this case, eggs that are very blue–green and brown. However, a recent study [17] on two species of thrushes (*Turdus* spp.) found that this was not the case. Instead, these hosts rejected brown eggs but accepted blue–green eggs, which would both be perceived as equally different from their own eggshell's colour. That is, they rejected eggs only on one side of their phenotypic range ('single threshold') [17]. Such a result could arise if hosts categorize eggshell colours during egg discrimination decisions, as has been demonstrated in birds in other contexts [18]. Regardless of the underlying mechanism, the optimal acceptance threshold hypothesis can be extended to accommodate a single threshold [19] and to identify novel decision rules that better explain host decisions. The natural avian eggshell colour gradient, varying from blue–green to brown [14], reduces trait dimensionality and, thus, makes bird egg coloration a valuable tool to explore such extensions of the optimal acceptance threshold hypothesis.

Colour is not the only important feature in egg discrimination decisions. The patterns generated through eggshell maculation, including spots and lines (hereafter, spots) are also important factors as they can generate unique egg signatures [20] that provide hosts with valuable information about egg ownership (own versus foreign) [21]. Hosts with spotted eggs are generally more likely to accept spotted foreign eggs, and hosts with unspotted eggs are generally more likely to

Figure 2. We painted pairs of three-dimensional printed [34] eggs along a phenotypic gradient of blue–green to brown, corresponding with natural variation in avian eggshell coloration across taxa [14], following [17]. After measuring the reflectance spectra of each egg, we (*a*) painted spots on one set and (*b*) left the other set unspotted. Here we depict 16 of 70 unique model eggs to demonstrate the range of colours and spotting patterns used. These eggs were placed within chalk-browed mockingbirds' nests (*c–h*) and the response of the host (either acceptance or rejection) was recorded over a 5-day period. Photo credit: A. V. López.

accept unspotted eggs [21,22]; in addition, spot colour, size, distribution and boundaries all provide valuable information to hosts [23,24]. The optimal acceptance threshold hypothesis predicts that when multiple components of the recognition cue are similar between stimuli (e.g. sharing colour and spotting rather than sharing either colour or spotting), their dissimilarity is decreased, and the likelihood of acceptance is greater [2]. For example, for a host with a spotted egg, the presence of spots on a foreign egg may be sufficient to shift it from the rejection side of the acceptance threshold to the acceptance side of the acceptance threshold, irrespective of that eggshell's coloration (figure 1). Thus, the optimal acceptance threshold hypothesis provides a framework for determining the relative contribution of individual components of multicomponent recognition cues to behavioural decisions.

We studied the chalk-browed mockingbird, *Mimus saturninus* (hereafter, mockingbird), which is a frequent host of the brood parasitic shiny cowbird *Molothrus bonariensis* (hereafter, cowbird) in South America. The mockingbird has a blue–green speckled egg (figure 1*b*), whereas the eggs of the cowbird are polymorphic [25], showing variation both in ground colour and in the density and distribution of the spots (figure 1*b*); cowbird eggs may be blue–green or white, or even brown if they are heavily spotted (figure 1*b*). Cowbirds reduce the fitness of the mockingbirds through puncturing host eggs [26–29] and through frequently engaging in multiple parasitism [30] (i.e. when more than one cowbird egg is found in the same nest). Mockingbirds actively defend their nests when parasites approach them [31] by vigorously mobbing the cowbirds [28], which can reduce the risk that the cowbird will puncture their eggs. In addition, mockingbirds also sometimes grasp-reject [28,32] (figure 1*c*) one specific cowbird egg morph: unspotted white cowbird eggs [22,32,33]. Since mockingbirds do not respond to variation within the colour range of spotted cowbird eggs [32], differential rejection responses to blue–green and brown eggs would be surprising. However, when choosing among a broader array of colours (e.g. the full extent of avian eggshell colours), it is feasible that mockingbirds will also preferentially reject browner model eggs. Such a finding would provide evidence that hosts in other genera also set a single acceptance threshold on one side of their eggshells' phenotypic range, as previously found in *Turdus* [17], and that this decision rule may be widespread among hosts of avian brood parasites.

To experimentally test colour-based egg discrimination in mockingbirds, we generated two sets of experimental egg models that varied identically along the span of natural eggshell coloration found across avian lineages (figure 2): from blue–green to brown [14]. Then, we added spots to one set of these experimental egg models. This generated a range of eggshell colours spanning the variation of real birds' eggshell colours, such that one set of eggs was more similar to the mockingbird eggs' own phenotype (spotted eggs) than the other set of eggs (unspotted eggs). By using this design, we tested whether mockingbirds applied a single threshold or multiple thresholds to colour-based egg discrimination decisions. If hosts applied multiple thresholds (set at both the bluer and browner side of their eggshell colour phenotypic range), we expected that mockingbirds would reject foreign eggs with a greater absolute perceived difference in eggshell colour from their own eggs. In this system, a host may face a parasite egg that is either bluer or browner than its own eggs (figure 1*b*); thus the application of multiple thresholds would prepare this host for either threat. Alternatively, if mockingbirds adhered to a single threshold decision rule, we expected that mockingbirds would reject brown eggs more than equally dissimilar blue–green eggs, as previously shown in other hosts [17]. This decision rule would expose hosts to threats from parasite eggs that are more blue–green than their own eggs, but may aid making rapid decisions when information is limited or uncertain [35,36] (e.g. when their clutch contains many parasite eggs). Finally, under either scenario, we expected that spotted eggs would be shifted towards the acceptance side (or region) of the acceptance threshold(s) relative to their unspotted counterparts, because for any given eggshell colour, spotted foreign eggs are more similar to the hosts' own eggs than unspotted eggs. By recording mockingbird egg rejection responses to these two sets of stimuli that vary along a natural phenotypic gradient, we quantified, in avian perceptual units, the contributions of both coloration and spotting toward egg rejection decisions.

2. Material and methods

(a) Experimental eggs

We ordered three-dimensional printed shiny cowbird egg models from shapeways.com (model: 6HVA2QYWW), using the previously described methods [34]. These models approximated the dimensions and mass of natural shiny cowbird eggs found at this site (*model egg* mean ± s.e.: (length × width) 22.6 ± 0.03 × 18.5 ± 0.02 mm, (mass) 3.3 ± 0.01 g, $n = 70$; *cowbird*: 23.2 ± 0.1 × 18.7 ± 0.1 mm, 4.26 ± 0.06 g, $n = 45$), which are both smaller than natural mockingbird eggs (28.2 ± 0.3 × 20.3 ± 0.2 mm; 6.1 ± 0.1 g, $n = 20$). We hand painted pairs of three-dimensional printed eggs to generate eggs that varied in the ground coloration along the natural gradient of avian eggshells (figure 2), following a previously published method [17], such that each colour was used twice. On one set of eggs, we applied a spotting pattern using a mixture of high-quality acrylic paint (Grumbacher burnt umber and Mars black). Our goal was to produce a consistent spotting pattern on the egg, rather than to perfectly replicate the variation in cowbird spot patterns or colours (electronic supplementary material, figures S1 and S2). To that end, we randomly chose a shiny cowbird egg from this population to serve as a template for spotting patterns and transferred that on clear plastic. Then, we projected that spot pattern on each egg from the spotted set and used an identical mixture of acrylic paint to apply (by hand) a standardized spot pattern within and between eggs. The spots on our experimental egg models were darker (electronic supplementary material, figures S1 and S2 and table S1), larger (electronic supplementary material, figures S1 and table S2), and more evenly distributed across the egg's surface than the spots found on either the cowbird or host eggs (electronic supplementary material, figure S1 and table S2); however, spotting patterns on experimental eggs were consistent (for more details see electronic supplementary material, figure S1 and table S3).

(b) Field methods

Our research was conducted at Reserva El Destino, near the town of Magdalena, in Buenos Aires Province, Argentina (35°08′ S, 57°23′ W), from November 2014 to January 2015. Following previously established protocols for this species [37], a single randomly selected experimental egg was chosen and added to a host's nest, and those nests were monitored for 5 days after the introduction of each model egg ($n = 85$). Model eggs that were still present at the end of the 5-day monitoring period were considered accepted and those that went missing during this period were considered rejected. We excluded deserted ($n = 9$, all after cowbird egg punctures) and predated nests ($n = 6$) from analyses [38], leaving a final sample size of 70 nests. In addition, we recorded a variety of potentially relevant covariates, including whether the parent was flushed [39] during the experimental introduction (yes: 6, no: 64), the experimental date as ordinal day (relative to the first egg in our dataset, such that 12 November 2014 = 1) [40], nest age at the time of the experiment (relative to clutch completion, such that an experiment 1 day before clutch completion = −1) [41], and the number of host eggs (mean ± s.e.: 2.1 ± 0.7) and natural cowbird eggs (1.1 ± 1.0) at the time of the experiment [41]. Although it is possible that a natural pure white cowbird egg was laid and then swiftly rejected without our knowledge (other cowbird eggs are always accepted, see above), we checked nests daily and any such bias would be equally probable for any nest. Additionally, we could not control for the possibility that some individuals in our population had more experience with natural cowbird eggs than other individuals; however, previous research suggests that the mockingbird does not reject spotted eggs [30,32], so we expect consistent responses across mated pairs regardless of their experience.

(c) Colour measurements and avian visual models

We measured the coloration of experimental egg models ($n = 70$), using an Ocean Optics Jaz spectrometer with a pulsed xenon light source (Jaz-PX) and a white reflectance standard (WS-1). The spectral reflectance of each egg was measured six times, prior to the addition of any spots, and we used the average reflectance spectrum to represent the colour of each egg. We also measured abandoned natural eggs of hosts ($n = 51$) and their parasites ($n = 60$) using an Ocean Optics 2000 reflectance spectrometer with a PX-2 pulsed xenon light source (Ocean Optics, Dunedin, Florida, USA), relative to a barium sulfate white standard, following [42,43]. The probe was consistently held 5 mm from the eggshell surface, at a 90° coincident normal measurement angle, for all measurements. Although we avoided spots wherever possible on natural eggshells, it was sometimes impossible to avoid including some fine spotting in our measurements, particularly on mockingbird eggs [14,44].

We smoothed each reflectance spectrum using a locally weighted polynomial prior to analysis. Then we applied a noise-limited discrimination model [45,46] to calculate the perceived difference in coloration and luminance (hereafter chromatic and achromatic contrasts, respectively) [45,47] between the average mockingbird eggshell coloration and that of each experimental egg, where the noise was calculated as the sum of neural and receptor noise [46]. As mockingbirds are phylogenetically placed among oscines with known ultraviolet (UV) visual sensitivity [48], we used the visual system of the average UV sensitive bird [49], and the blue tit, *Cyanistes caeruleus*, double cone sensitivity [50]. Because mockingbirds nest within and under scrub or tree foliage [51], these visual models assumed a filtered forest light [52] scaled to simulate bright viewing conditions [53]. These analyses resulted in estimates of perceivable differences in just noticeable difference (JND) units, where values less than 1.0 would not be noticeably different, values of 1.0 would be just noticeable under ideal conditions, and as values become increasingly larger than 1.0 those differences become increasingly discernible. These JND thresholds are theoretical, such that actual discriminability thresholds may differ [54]; however, the exact threshold does not affect our findings, as our goal was to generate a range of discriminable differences.

We painted eggs such that the ground colour between spotted and unspotted eggs of each pair was similar (chromatic contrast = 0.26 ± 0.03 JND, achromatic contrast = 0.52 ± 0.05 JND, $N = 70$). By contrast, our experimental colours expanded the natural variation in eggshell colour [14,17] and ranged from similar to noticeably different from natural mockingbird (chromatic contrast range = 0.76 to 8.32 JND; achromatic contrast range = 0.01 to 13.78 JND) and cowbird eggshell colours (chromatic contrast range = 1.85 to 8.62 JND; achromatic contrast range = 3.51 to 16.81 JND). However, every real host egg was similar to at least one experimental egg model's colour and luminance (mean ± s.e. of the closest match for chromatic contrast = 1.44 ± 0.05 JND; achromatic contrast = 3.52 ± 0.26). These differences were similar to the average perceivable differences between host and cowbird eggshell colour (chromatic contrast = 1.34 ± 0.04 JND, $t_{100} = -1.49$, $p = 0.14$) and luminance (achromatic contrast = 3.63 ± 0.24, $t_{100} = 0.29$, $p = 0.77$), respectively.

We also calculated each model egg's position within the avian tetrahedral colour space [55,56] to determine if mockingbirds would perceive each experimental egg as more blue–green (i.e. closer to the short-wave sensitive photoreceptor) or browner (i.e. closer to the long-wave sensitive photoreceptor) than their average egg colour. Although we recognize that abandoned eggs may fade [57], we assumed that these abandoned eggs provided a reasonable estimate of host eggshell colour; mockingbirds do not respond to the vast majority of cowbird parasitism, and it is unlikely that those laying a particular colour egg would produce a particular type of response. To test egg rejection along the blue–green to brown eggshell colour gradient, the JNDs between bluer eggs and the average host egg were multiplied by −1, while JNDs between browner eggs and the average host egg were multiplied by 1. All colour and perceptual modelling analyses were conducted using the 'pavo' package [58] in the programing language R.

(d) Statistical analyses

We examined differences in rejection rates between spotted and unspotted eggshells first using Fisher's exact tests, which we report through their associated odds ratios (OR) and 95% confidence intervals (CI). We then examined mockingbird rejection behaviours using a generalized linear model (GLM), using the '*glm*' function in the '*stats*' package within the R environment for statistical computing [59]. Since host responses were either 'accept' or 'reject', we used a binomial distribution with a logit link function. We calculated the significance of whole models by comparing each parametrized model with a null model including just the intercept [60]. We generated two models to test whether host responses were better explained by the multiple threshold rule or the single threshold rule. First, to test the multiple threshold rule, we predicted host response by absolute perceivable differences in coloration (chromatic contrast, continuous in JND units), the presence or absence of spots (categorical: yes or no), and the number of cowbird eggs at the time of the experiment (continuous). Here, large chromatic contrast values correspond with eggs that were either bluer or browner than the average mockingbird egg. Second, to test the single threshold rule, we constructed an identical model but included directional colour differences varying from blue–green to brown (directional colour differences, continuous in JND units) instead of chromatic contrasts. Here, large directional colour differences correspond with eggs that are browner than the average mockingbird egg.

In addition, we performed an additional analysis (see supplementary material, table S4) to explore the potential role of a range of covariates by constructing a global model including the variables above as well as a range of covariates: whether the host was flushed from the nest (categorical: yes or no), nest age at the time of the experiment (continuous, hatching date = day 0), the number of host eggs (continuous) at the time of the experiment, and the experiment date (continuous). This model included an interaction to explicitly consider the possibility that hosts responded differently to directional colour differences (e.g. along a different response curve) between spotted and unspotted eggs. For example, hosts may accept all spotted eggs (regardless of their colour), but they may reject brown unspotted eggs and accept blue–green unspotted eggs. We then performed a backward-elimination selection procedure, by sequentially removing the covariate with the largest non-significant p-values, and rerunning the model with the remaining covariates until a final model including only significant predictors remained [61].

All continuous variables were centred and scaled prior to analyses and to aid the comparison of individual parameters and their interactions [62]. As an estimate of the goodness of fit, we report Nagelkerke's R^2 [63] and the corrected Akaike's information criterion ($\mathrm{AIC_c}$) [63,64] for each model. We compared the predictive power of multiple models using $\mathrm{AIC_c}$-based evidence ratios [65,66]. Unfortunately, owing to the colours of available paints, and the properties of subtractive colour mixing, despite our best efforts, avian perceived brightness covaried across the colour gradient such that browner eggs were darker; so achromatic contrast and directional colour differences were positively correlated ($r = 0.82$, $\mathrm{CI}_{0.95} = 0.73$ to 0.89, $n = 70$, $p < 0.0001$). Therefore, to avoid multicollinearity, we did not include achromatic contrasts in our statistical models. Instead, to determine whether host responses were better predicted by achromatic contrast or directional colour differences, we examined the independent effects of these predictors to explain host responses using a subsampling procedure. Specifically, we randomly sampled a subset of the rejection dataset ($n = 35$) 1000 times, and for each sample we conducted separate GLMs predicting host response by either achromatic contrast or directional colour differences. We then compared the sampled standardized effect estimates from these models using two-tailed paired t-tests. We also compared the sampled p-values using similar t-tests. As an additional method of comparison, and to parallel the analysis with achromatic contrasts, we provide similar tests to evaluate the relative importance of perceived differences between foreign and host eggs in terms of absolute perceived colour differences (i.e. chromatic contrast) and directional colour differences (i.e. how much bluer or browner a foreign egg is relative to that of the host). All analyses were conducted in R v. 3.1.2 [59]. All data are presented as mean ± standard error.

3. Results

At our study site, 67% of the monitored mockingbird nests were naturally parasitized by cowbird eggs; the subset of parasitized nests had a parasitism intensity of 1.6 ± 0.1 cowbird eggs per nest (range: 1–4) and we did not detect any rejection of natural cowbird eggs in this study. We detected a 45.7% rejection rate for experimental eggs ($n = 32$ of 70 eggs); however, unspotted eggs were rejected in 58.3% of trials ($n = 21$ of 36 eggs) and spotted eggs were rejected only 32.4% of the time ($n = 11$ of 34 eggs). These differences in egg ejection responses demonstrate that the likelihood of a mockingbird rejecting an unspotted egg is greater than the likelihood of rejecting a spotted egg (OR = 0.35, $\mathrm{CI}_{0.95} = 0.11$–$1.01$, $p = 0.03$), which corresponds to the results of separate GLMs (table 1).

Contrary to our expectations of host responses under a multiple threshold decision rule, we found that host

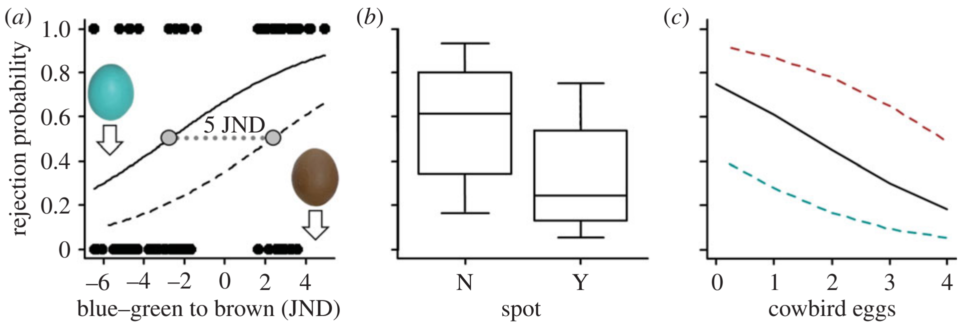

Figure 3. The probability of rejecting an experimental egg as predicted by the main effects: (*a*) variation in experimental egg colour, (*b*) spot absence (N) or presence (Y), and (*c*) the number of cowbird eggs in the nest at the time of the experiment. A binomial GLM predicted that mockingbird (*a*) behavioural responses (black dots; accept = 0.0, eject = 1.0) were biased toward rejecting brown unspotted (solid line) and spotted (dashed line) model eggs; however, the behavioural responses to these model eggs differed such that they were likely to reject an unspotted foreign egg at the 50% level if it was 2.71 JND bluer than their own, but if the egg was spotted it would need to be 2.31 JND browner (see grey circles connected by grey dotted line) than their own egg to illicit the same response. In general (*b*), unspotted model eggs were more likely to be rejected than spotted eggs. Similarly, mockingbirds were (*c*) more likely to respond to experimental parasitism when they had fewer natural parasitic cowbird eggs in the nest. Here we represent predicted rejection probability of model eggs versus the number of natural cowbird eggs for an egg model of the average colour (solid line), as well as for egg models with colours below (the lower dashed blue–green line) and above (the upper dashed brown line) the lower and upper 95% confidence limits for sampled colour variation. As the number of real cowbird eggs increased in the clutch, and dominated the nest, hosts were less likely to reject the experimental model egg. (Online version in colour.)

Table 1. Generalized linear models predicting the probability of mockingbirds rejecting foreign egg models based on either multiple or single thresholds. We present Nagelkerke's R^2 and AIC$_c$ for whole models, parameter estimates representing the change in log-odds and their associated standard errors (s.e.), the lower and upper limits of the 95% confidence interval (LCL and UCL), a measure of standardized effect (*z*-score) and variance inflation factors (VIF) for all parameters. 'Directional colour' represents the change in log-odds of rejecting egg models that are 1.0 just noticeable difference (JND) more blue–green (negative) or browner (positive) than the average mockingbird egg. 'Chromatic contrast' and 'achromatic contrast' represent the difference in perceivable coloration and brightness between egg models and the average mockingbird egg, respectively (see Methods for full details). 'Cowbird eggs' represents the number of cowbird eggs at the time of experimentation. 'Spot' is coded as unspotted (0) or spotted (1). Significant models and effects are italicized.

decision rule	predictor	estimate	s.e.	LCL	UCL	*z*	χ^2	d.f.	*p*-value	VIF
multiple	*full model* ($\chi^2 = 11.80$, $R^2 = 0.21$, AIC$_c = 93.34$, $p = 0.008$)									
threshold	*intercept*	*1.78*	*0.85*	*0.19*	*3.56*	*2.09*	—	*1*	*0.04*	—
	chromatic contrast	−0.22	0.20	−0.63	0.17	−1.09	1.21	1	0.27	1.02
	spot	*−1.20*	*0.53*	*−2.28*	*−0.18*	*−2.25*	*5.36*	*1*	*0.02*	*1.03*
	cowbird eggs	*−0.63*	*0.29*	*−1.23*	*−0.09*	*−2.16*	*5.21*	*1*	*0.02*	*1.02*
single	*reduced model* ($\chi^2 = 21.34$, $R^2 = 0.35$, AICc $= 83.80$, $p < 0.0001$)									
threshold	intercept	0.43	0.39	−0.33	1.22	1.09		1	0.28	—
	directional colour	*0.91*	*0.30*	*0.36*	*1.53*	*3.07*	*10.76*	*1*	*<0.01*	*1.04*
	spot	*−1.31*	*0.58*	*−2.51*	*−0.21*	*−2.25*	*5.46*	*1*	*0.02*	*1.05*
	cowbird eggs	*−0.64*	*0.29*	*−1.25*	*−0.09*	*−2.20*	*5.26*	*1*	*0.02*	*1.03*

responses were predicted by spot presence and the number of cowbird eggs at the time of the experiment, but not chromatic contrast (table 1). By contrast, a similarly constructed model supported our expectations of host response under a single threshold decision rule. Specifically, host responses were significantly predicted by directional colour differences (figure 3*a*), spot presence (figure 3*b*) and the number of cowbird eggs at the time of the experiment (figure 3*c*). In fact, evidence ratios suggest that this model predicted host behaviour 118 times better than one based on absolute perceptual distances, i.e. chromatic contrast (table 1). This model was corroborated through a stepwise selection procedure that found that host responses were best predicted by directional colour differences, whether the experimental egg was spotted and how many cowbird eggs were present in the nest at the time of the experiment (electronic supplementary material, table S4). Furthermore, our resampling procedure found that directional differences in colour (i.e. how much bluer or browner the experimental egg was relative to that of the host) explained host responses significantly better than chromatic contrast (directional colour $\beta = 0.46 \pm 0.002$, chromatic contrast $\beta = -0.18 \pm 0.008$, $t_{999} = 102.70$, $p < 0.0001$; directional colour $p < 0.0001 \pm {<}0.0001$, chromatic contrast $p = 0.54 \pm 0.008$, $t_{999} = -63.15$, $p < 0.0001$; see standardized effects in table 1). Importantly, we found no significant interaction, suggesting that the application of eggshell spots shifted eggs to the acceptance side of the acceptance threshold, but the mockingbird's response to colour variation otherwise followed a similar sigmoidal function (figure 3*a*). These findings demonstrate that mockingbirds preferentially rejected brown eggs (both spotted and unspotted), and were more permissive of spotted eggs and more restrictive of unspotted eggs. Specifically, the colour that would result in an experimental egg model being rejected 50% of the time differed by 5.0 JND between spotted and unspotted eggs (figure 3*a*). Although directional colour differences were related to perceived brightness, our resampling analyses demonstrate that directional colour differences significantly predicted host response but achromatic contrasts did not (directional colour $\beta = 0.46 \pm 0.002$, achromatic contrast $\beta = -0.24 \pm 0.01$, $t_{999} = 86.93$, $p < 0.0001$; directional colour $p < 0.0001 \pm <0.0001$, achromatic contrast $p = 0.50 \pm 0.009$, $t_{999} = -57.05$, $p < 0.0001$; electronic supplementary material, figure S3). In other words, although browner egg models were also darker, there is no statistical evidence that this affected the likelihood of egg rejection, as directional colour differences predicted host responses better than perceived differences in brightness.

4. Discussion

Optimal acceptance threshold theory has been successfully applied to predict the direction of shifts in egg rejection decisions in several different hosts of avian brood parasites [6,67,68]. However, no study has quantified the extent to which individual components of a recognition cue (such as colour or spotting) can shift a stimulus toward the acceptance or rejection side of the acceptance threshold. Here we measured how mockingbirds responded to spotted or unspotted model cowbird eggs coloured along a gradient corresponding with natural avian eggshell coloration (figure 3). We discovered that host responses were not explained by the absolute perceived differences between their own and foreign eggs, which is often assumed by tests of the optimal acceptance threshold hypothesis. Instead, our findings demonstrate that mockingbirds in South America, similar to egg rejecter *Turdus* thrushes in North America and Europe [17], are biased toward rejecting brown eggs over blue–green (figure 3). However, as predicted by the optimal acceptance threshold hypothesis, when the discrimination task was made more challenging by experimentally increasing the similarity between foreign eggs (through the addition of spotting), rejection responses became less likely. Specifically, eggshell spots made these foreign eggs more similar to the hosts' own phenotype (for every particular eggshell colour tested in our experiment). As predicted, the addition of spots shifted eggs to the 'acceptance' side of the acceptance threshold.

Tests of the optimal acceptance threshold theory generally assume that hosts will respond to absolute perceived dissimilarity between the hosts' own and foreign eggs [2]; therefore, it is surprising that hosts rejected eggs browner than their own and accepted eggs more blue–green than their own, even if these had the same absolute perceived differences from the bird's own egg colour (or its internal template representation [69]). Although it is possible that dark brown eggs are more cryptic and therefore more difficult to detect in the nest [70], we found that these eggs were rejected at higher rates, suggesting this alternative is unlikely in this case. The data from the current study are consistent with the findings of a previous study examining the responses of European blackbirds, *Turdus merula*, and American robins, *T. migratorius*, to egg models coloured along the same blue–green to brown eggshell colour gradient [17]. In addition to providing meta-replication in a third species, our new findings demonstrate meta-replication of these patterns in a third continent (South America, in addition to Europe and North America) and a third brood parasite species (the shiny cowbird, in addition to conspecific European blackbird and interspecific brown-headed cowbird *Molothrus ater* parasitism [17]). These findings consistently challenge the long-held assumption that hosts use absolute perceivable colour differences between their own and the foreign eggs (reviewed in [16]). Instead, such decisions could be produced if hosts use colour categorization; if hosts' internal templates are bluer than their own eggs are; or if hosts use a currently unknown cognitive mechanism for egg discrimination [71]. Thus, the underlying mechanism of colour-based egg discrimination, across diverse host species in different types of brood parasitism, deserves greater attention. We encourage the development of novel hypotheses as well as new and more consistent methodologies [72] for research examining the phenotypic and cognitive bases of egg rejection decisions.

The mockingbird's main defence against parasitism is mobbing, although they are generally unable to prevent parasitic egg laying or to reject parasitic cowbird eggs once laid [28]. The exception, however, is that mockingbirds will predictably reject natural, unspotted white cowbird eggs [22], which may be because they are unlike their own eggs in two components of eggshell appearance: coloration and spots [22]. Although this suggests that mockingbirds do not discriminate eggs based on colour, we found that mockingbirds have strong rejection responses to (even spotted) foreign egg models browner than their own. Thus, mockingbirds do have the ability to discriminate models of parasitic eggs based on their colour alone, even though when confronted with natural parasitism these discrimination abilities are generally not exercised. In addition, we demonstrate the importance of both eggshell colour and spotting on rejection decisions in this species. We found that a spotted egg could be up to 5.0 JND browner than an unspotted egg but still have the same likelihood of being rejected (figure 3*a*). In fact, for the brownest pair of eggs (which were the most likely to be rejected; figure 2), the unspotted brown egg resulted in a higher rejection rate (greater than 80%) than the spotted egg (approx. 60%; figure 3*a*). By contrast, the pair of eggs that were the most blue–green (figure 2) both had low rejection rates, but again, the unspotted blue–green eggs were more likely to be rejected (approx. 30%) than the spotted blue–green egg (less than 10%; figure 3*a*). Our findings suggest that this host has not yet adapted the ability to discriminate fine-grained differences in eggshell patterns, but instead uses eggshell features as an all-or-nothing cue. Although it is possible that artificial eggs with spots were more cryptic and thus harder to detect [73] in mockingbird nests, this is unlikely because rejection probability was predicted by eggshell colour variation within spotted eggs (the phenotype that is theoretically most cryptic, spotted brown eggs, was rejected at the highest rates). Moreover, the spotting patterns on mockingbird eggs differ from those of the cowbird (figure 1*b* and electronic supplementary material, figure S1*c*), which suggests that the amount of spotting and the exact spotting pattern do not necessarily impact host response. Nonetheless, we encourage future research to explore whether and how a host's perception of fine-grained spot patterns may lead to shifts in rejection decisions [20].

Within our study area, shiny cowbird females lack territoriality [74] and mockingbird nests are often parasitized by multiple cowbirds [28,75]. When hosts are parasitized multiple times, discriminating the parasitic egg from the host's own becomes more challenging and requires greater perceivable differences in eggshell phenotypes to elicit a response [76,77]. This was experimentally demonstrated in great reed warblers, *Acrocephalus arundinaceus*, [69] and the tawny-flanked prinia, *Prinia subflava*, [76], which are hosts to the common cuckoo, *Cuculus canorus*, and the cuckoo finch, *Anomalospiza imberbis*, respectively. Similarly, we found that when mockingbirds faced a greater number of natural shiny cowbird eggs in their clutch, they were less likely to reject the foreign egg models. Thus, our results suggest that engaging in multiple parasitism and laying spotted eggshells provide a substantial advantage to shiny cowbirds to avoid egg rejection by chalk-browed mockingbirds, and therefore multiple parasitism and eggshell spotting are likely to be under strong selective pressure in this shiny cowbird population. Similarly, cowbirds that lay spotted blue–green eggs in mockingbird nests should have a selective advantage over those laying other morphs; nonetheless, several other egg morphs persist in this population [30,78]. We encourage future research to examine whether colour-biased egg discrimination could play a role in regulating natural cowbird egg morphs.

We demonstrated that mockingbird responses are biased toward rejecting browner eggs, rather than being based upon absolute perceivable differences in eggshell colour. Contrary to the assumptions often applied to the acceptance threshold hypothesis, this host did not respond to the degree of dissimilarity between their eggs and foreign eggs *per se*. Instead, this host rejected brown eggs but accepted equally dissimilar blue–green eggs. These patterns suggest important and unexplored aspects of co-evolutionary dynamics within the chalk-browed mockingbird–shiny cowbird system, and host–parasite dynamics more generally. Moreover, these findings suggest that this unnecessary, though often applied, assumption to the acceptance threshold hypothesis is limiting our full exploration of its versatility. We illustrate that decision-making is not always adequately predicted simply by perceptual distances and that the acceptance threshold hypothesis should not be restricted by such assumptions. Additionally, as predicted by the acceptance threshold hypothesis, when the uncertainty of that decision was altered by the experimental addition of spots (i.e. reducing the overall trait dissimilarity, figure 1*a*) or the increased number of natural parasitic eggs (figure 3*c*), the likelihood of egg rejection was reduced. By using a simple experimental design with treatments (spotted or unspotted) varying along the same continuous range of ground colours, we were able to effectively measure (in avian perceivable units) the degree to which spots contributed to eggshell appearance.

Colour-biased responses might be expected if hosts use colour categorization for egg discrimination tasks, as has been demonstrated in birds in other contexts [79]. Previous research [17] found that hosts were more adept at differentiating differences between blue–green and brown eggs than within either colour category, despite the absolute perceivable differences within or between groups [17], which is a defining feature of categorical perception [80–82]. In this study, birds similarly produced differential responses to eggs more blue–green or browner than their own. Together, these findings suggest that hosts may use colour categorization as the basis for rejection decisions [17], which would potentially allow hosts, even naive hosts, to make rapid decisions [18] in the absence of other information or experience detecting parasitic eggs or under conditions when the information is uncertain [35,80,83]. Although further research is required to confirm the underlying mechanism explaining these behaviours, our research does demonstrate that decision boundaries can be set throughout the phenotypic range and that specific components of a multicomponent cue can shift the position of those decision boundaries. This finding, from a wild population, has important implications for future investigations to determine how decision boundaries are set when information is uncertain [36]. Lastly, given these findings, we recommend that the theoretical models we use to study animal decision-making should be as flexible and varied as the decision rules employed by the decision-makers themselves.

Ethics. The study was conducted with the permission of the Provincial Organism for Sustainable Development (OPDS, Buenos Aires, Argentina; permit no. 202/12-O.P.D.S.) and complies with the current laws of Argentina.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. D.H. and M.E.H. designed the field study. V.D.F. coordinated the study in Argentina and supervised the field research. A.V.L. collected field data. J.C.R. supervised the general project in Argentina. D.H. conducted the statistical analyses. T.G. provided advice throughout. DH wrote the initial draft. All co-authors contributed to writing and editing.

Competing interests. We declare we have no competing interests.

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References

1. Mendelson TC, Shaw KL. 2012 The (mis)concept of species recognition. *Trends Ecol. Evol.* **27**, 421–427. (doi:10.1016/j.tree.2012.04.001)
2. Reeve HK. 1989 The evolution of conspecific acceptance thresholds. *Am. Nat.* **133**, 407. (doi:10.1086/284926)
3. Leonard AS, Dornhaus A, Papaj DR. 2011 Flowers help bees cope with uncertainty: signal detection and the function of floral complexity.

J. Exp. Biol. **214**, 113–121. (doi:10.1242/jeb.047407)

4. Engel KC, Ayasse M, Manner L, Steiger S. 2015 Acceptance threshold theory can explain occurrence of homosexual behaviour. *Biol. Lett.* **11**, 1–4. (doi:10.1098/rsbl.2014.0603)
5. Starks PT, Fischer DJ, Watson RE, Melikian GL, Nath SD. 1998 Context-dependent nestmate discrimination in the paper wasp, *Polistes dominulus*: a critical test of the optimal acceptance threshold model. *Anim. Behav.* **56**, 449–458. (doi:10.1006/anbe.1998.0778)
6. Hauber ME, Moskát C, Bán M. 2006 Experimental shift in hosts' acceptance threshold of inaccurate-mimic brood parasite eggs. *Biol. Lett.* **2**, 177–180. (doi:10.1098/rsbl.2005.0438)
7. Davies NB, Brooke ML. 1989 An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. *J. Anim. Ecol.* **58**, 207–224. (doi:10.2307/4995)
8. Feeney WE, Welbergen JA, Langmore NE. 2014 Advances in the study of coevolution between avian brood parasites and their hosts. *Annu. Rev. Ecol. Evol. Syst.* **45**, 227–246. (doi:10.1146/annurev-ecolsys-120213-091603)
9. Kilner RM, Madden JR, Hauber ME. 2004 Brood parasitic cowbird nestlings use host young to procure resources. *Science* **305**, 877–879. (doi:10.1126/science.1098487)
10. Peer BD, Rothstein SI, Kuehn J, Fleischer RC. 2005 Host defenses against cowbird (*Molothrus ater*) parasitism: implications for cowbird management. *Ornithol. Monogr.* **57**, 84–97. (doi:10.2307/40166816)
11. Sealy SG. 1995 Burial of cowbird eggs by parasitized yellow warblers: an empirical and experimental study. *Anim. Behav.* **49**, 877–889. (doi:10.1006/anbe.1995.0120)
12. Igic B *et al.* 2015 A nanostructural basis for gloss of avian eggshells. *J. R. Soc. Interface* **12**, 20141210. (doi:10.1098/rsif.2014.1210)
13. Fecheyr-Lippens DC *et al.* 2015 The cuticle modulates ultraviolet reflectance of avian eggshells. *Biol. Open* **4**, 753–759. (doi:10.1242/bio.012211)
14. Hanley D, Grim T, Cassey P, Hauber ME. 2015 Not so colourful after all: eggshell pigments constrain avian eggshell colour space. *Biol. Lett.* **11**, 20150087. (doi:10.1098/rsbl.2015.0087)
15. Kennedy GY, Vevers HG. 1976 A survey of avian eggshell pigments. *Comp. Biochem. Physiol.* **55**, 117–123.
16. Hauber ME *et al.* 2015 The value of artificial stimuli in behavioral research: making the case for egg rejection studies in avian brood parasitism. *Ethology* **121**, 521–528. (doi:10.1111/eth.12359)
17. Hanley D, Grim T, Igic B, Samaš P, López AV, Shawkey MD, Hauber ME. 2017 Egg discrimination along a gradient of natural variation in eggshell coloration. *Proc. R. Soc. B* **284**, 20162592. (doi:10.1098/rspb.2016.2592)
18. Nelson DA, Marler P. 1989 Categorical perception of a natural stimulus continuum: birdsong. *Science* **244**, 976–978. (doi:10.1126/science.2727689)
19. Rodríguez-Gironés MA, Lotem A. 1999 How to detect a cuckoo egg: a signal-detection theory model for recognition and learning. *Am. Nat.* **153**, 633–648.
20. Stoddard MC, Kilner RM, Town C. 2014 Pattern recognition algorithm reveals how birds evolve individual egg pattern signatures. *Nat. Commun.* **5**, 4117. (doi:10.1038/ncomms5117)
21. Dainson M, Hauber ME, López AV, Grim T, Hanley D. 2017 Does contrast between eggshell ground and spot coloration affect egg rejection? *Sci. Nat.* **104**, 54. (doi:10.1007/s00114-017-1476-2)
22. de la Colina MA, Pompilio L, Hauber ME, Reboreda JC, Mahler B. 2012 Different recognition cues reveal the decision rules used for egg rejection by hosts of a variably mimetic avian brood parasite. *Anim. Cogn.* **15**, 881–889. (doi:10.1007/s10071-012-0515-9)
23. Stoddard MC, Stevens M. 2011 Avian vision and the evolution of egg color mimicry in the common cuckoo. *Evolution* **65**, 2004–2013. (doi:10.1111/j.1558-5646.2011.01262.x)
24. Spottiswoode CN, Stevens M. 2010 Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proc. Natl Acad. Sci. USA* **107**, 8672–8676. (doi:10.1073/pnas.0910486107)
25. Ortega CP. 1998 *Cowbirds and other brood parasites*. Tuscon, AZ: University of Arizona Press.
26. Massoni V, Reboreda JC. 1999 Egg puncture allows shiny cowbirds to assess host egg development and suitability for parasitism. *Proc. R. Soc. Lond. B* **266**, 1871–1874. (doi:10.1098/rspb.1999.0859)
27. Astié AA, Reboreda JC. 2009 Shiny cowbird parasitism of a low quality host: effect of host traits on a parasite's reproductive success. *J. Field Ornithol.* **80**, 224–233. (doi:10.1111/j.1557-9263.2009.00225.x)
28. Gloag R, Fiorini VD, Reboreda JC, Kacelnik A. 2012 Brood parasite eggs enhance egg survivorship in a multiply parasitized host. *Proc. R. Soc. Lond. B* **279**, 1831–1839. (doi:10.1098/rspb.2011.2047)
29. Fiorini VD, Tuero DT, Reboreda JC. 2009 Shiny cowbirds synchronize parasitism with host laying and puncture host eggs according to host characteristics. *Anim. Behav.* **77**, 561–568. (doi:10.1016/j.anbehav.2008.11.025)
30. Gloag R, Fiorini VD, Reboreda JC, Kacelnik A. 2014 Shiny cowbirds share foster mothers but not true mothers in multiply parasitized mockingbird nests. *Behav. Ecol. Sociobiol.* **68**, 681–689. (doi:10.1007/s00265-014-1682-2)
31. Gloag R, Fiorini VD, Reboreda JC, Kacelnik A. 2013 The wages of violence: mobbing by mockingbirds as a frontline defence against brood-parasitic cowbirds. *Anim. Behav.* **86**, 1023–1029. (doi:10.1016/j.anbehav.2013.09.007)
32. Sackmann P, Reboreda JC. 2003 A comparative study of shiny cowbird parasitism of two large hosts, the chalk-browed mockingbird and the rufous-bellied thrush. *Condor* **105**, 728. (doi:10.1650/7194)
33. Fraga RM. 1985 Host-parasite interactions between chalk-browed mockingbirds and shiny cowbirds. *Ornithol. Monogr.* **36**, 829–844. (doi:10.2307/40168319)
34. Igic B *et al.* 2015 Using 3D printed eggs to examine the egg-rejection behaviour of wild birds. *PeerJ* **3**, e965. (doi:10.7717/peerj.965)
35. Kepecs A, Uchida N, Zariwala HA, Mainen ZF. 2008 Neural correlates, computation and behavioural impact of decision confidence. *Nature* **455**, 227–231. (doi:10.1038/nature07200)
36. Qamar AT, Cotton RJ, George RG, Beck JM, Prezhdo E, Laudano A, Tolias AS, Ma WJ. 2013 Trial-to-trial, uncertainty-based adjustment of decision boundaries in visual categorization. *Proc. Natl Acad. Sci. USA* **110**, 20332–20337. (doi:10.1073/pnas.1219756110)
37. Reboreda JC, Fiorini VD, Mársico MC. 2013 Antiparasitic defenses in hosts of South American cowbirds. *Chinese Birds* **4**, 57–70. (doi:10.5122/cbirds.2013.0003)
38. Hauber ME, Samaš P, Anderson MG, Rutila J, Low J, Cassey P, Grim T. 2014 Life-history theory predicts host behavioural responses to experimental brood parasitism. *Ethol. Ecol. Evol.* **26**, 349–364. (doi:10.1080/03949370.2013.851121)
39. Hanley D, Samaš P, Heryán J, Hauber ME, Grim T. 2015 Now you see it, now you don't: flushing hosts prior to experimentation can predict their responses to brood parasitism. *Sci. Rep.* **5**, 9060. (doi:10.1038/srep09060)
40. Brooke MDL, Davies NB, Noble DG. 1998 Rapid decline of host defences in response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing world. *Proc. R. Soc. Lond. B* **265**, 1277–1282. (doi:10.1098/rspb.1998.0430)
41. Moskát C, Hauber ME. 2007 Conflict between egg recognition and egg rejection decisions in common cuckoo (*Cuculus canorus*) hosts. *Anim. Cogn.* **10**, 377–386. (doi:10.1007/s10071-007-0071-x)
42. Osorio D, Ham AD. 2002 Spectral reflectance and directional properties of structural coloration in bird plumage. *J. Exp. Biol.* **205**, 2017–2027. (doi:10.1242/jeb.01988)
43. Facchinetti C, Reboreda JC. 2013 Female tawny-bellied seedeaters do not prefer more colorful males in choice experiments. *J. Ethol.* **31**, 233–238. (doi:10.1007/s10164-013-0371-3)
44. Hanley D, Cassey P, Doucet SM. 2013 Parents, predators, parasites, and the evolution of eggshell colour in open nesting birds. *Evol. Ecol.* **27**, 593–617. (doi:10.1007/s10682-012-9619-6)
45. Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill IC. 1998 Tetrachromacy, oil droplets and bird plumage colours. *J. Comp. Physiol. A* **183**, 621–633. (doi:10.1007/s003590050286)
46. Vorobyev M, Osorio D. 1998 Receptor noise as a determinant of colour thresholds. *Proc. R. Soc. Lond. B* **265**, 351–358. (doi:10.1098/rspb.1998.0302)
47. Siddiqi A, Cronin TW, Loew ER, Vorobyev M, Summers K. 2004 Interspecific and intraspecific views of color signals in the strawberry poison frog

Dendrobates pumilio. *J. Exp. Biol.* **207**, 2471–2485. (doi:10.1242/jeb.01047)

48. Aidala Z *et al.* 2012 Ultraviolet visual sensitivity in three avian lineages: paleognaths, parrots, and passerines. *J. Comp. Physiol. A* **198**, 495–510. (doi:10.1007/s00359-012-0724-3)
49. Endler JA, Mielke PW. 2005 Comparing entire colour patterns as birds see them. *Biol. J. Linn. Soc.* **86**, 405–431. (doi:10.1111/j.1095-8312.2005.00540.x)
50. Hart NS, Partridge JC, Cuthill IC, Bennett ATD. 2000 Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (*Parus caeruleus* L.) and the blackbird (*Turdus merula* L.). *J. Comp. Physiol. A* **186**, 375–387. (doi:10.1007/s003590050437)
51. Fiorini VD, Tuero DT, Reboreda JC. 2009 Host behaviour and nest-site characteristics affect the likelihood of brood parasitism by shiny cowbirds on chalk-browed mockingbirds. *Behaviour* **146**, 1387–1403. (doi:10.1163/156853909X433338)
52. Endler JA. 1993 The color of light in forests and its implications. *Ecol. Monogr.* **63**, 1–27. (doi:10.2307/2937121)
53. Vorobyev M. 2003 Coloured oil droplets enhance colour discrimination. *Proc. R. Soc. Lond. B* **270**, 1255–1261. (doi:10.1098/rspb.2003.2381)
54. Hempel N, Giurfa M, Vorobyev M, de Ibarra NH, Giurfa M, Vorobyev M. 2002 Discrimination of coloured patterns by honeybees through chromatic and achromatic cues. *J. Comp. Physiol. A* **188**, 503–512. (doi:10.1007/s00359-002-0322-x)
55. Stoddard MC, Prum RO. 2008 Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of New World buntings. *Am. Nat.* **171**, 755–776. (doi:10.1086/587526)
56. Goldsmith TH. 1990 Optimization, constraint, and history in the evolution of eyes. *Q. Rev. Biol.* **65**, 281–322. (doi:10.1086/416840)
57. Hanley D, Šulc M, Brennan PLRPLR, Hauber MEME, Grim T, Honza M. 2016 Dynamic egg color mimicry. *Ecol. Evol.* **6**, 4192–4202. (doi:10.1002/ece3.2187)
58. Maia R, Eliason CM, Bitton P, Doucet SM, Shawkey MD. 2013 pavo: an R package for the analysis, visualization and organization of spectral data. *Methods Ecol. Evol.* **4**, 906–913. (doi:10.1111/2041-210X.12069)
59. R Development Core Team. 2014 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org.
60. Zuur AF, Hilbe JM, Ieno EN. 2013 *A beginner's guide to GLM and GLMM with R: a frequentist and Bayesian perspective for ecologists*, 1st edn. Newburgh, UK: Highland Statistics.
61. Grafen A, Hails R. 2002 *Modern statistics for the life sciences*. Oxford, UK: Oxford University Press.
62. Schielzeth H. 2010 Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**, 103–113. (doi:10.1111/j.2041-210X.2010.00012.x)
63. Nagelkerke NJD. 1991 A note on a general definition of the coefficient of determination. *Biometrika* **78**, 691–692. (doi:10.1093/biomet/78.3.691)
64. Peng C-YJ, Lee KL, Ingersoll GM. 2002 An introduction to logistic regression analysis and reporting. *J. Educ. Res.* **96**, 3–14. (doi:10.1080/00220670209598786)
65. Wagenmakers E, Farrell S. 2004 AIC model selection using Akaike weights. *Psychon. Bull. Rev.* **11**, 192–196. (doi:10.3758/BF03206482)
66. Burnham KPKP, Anderson DRDR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. New York, NY: Springer.
67. Davies NB, Brooke ML, Kacelnik A. 1996 Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proc. R. Soc. B* **263**, 925–931. (doi:10.1098/rspb.1996.0137)
68. Mermoz ME, Haupt C, Fernández GJ. 2015 Brown-and-yellow marshbirds reduce their acceptance threshold of mimetic brood parasite eggs in the presence of non-mimetic eggs. *J. Ethol.* **34**, 65–71. (doi:10.1007/s10164-015-0447-3)
69. Bán M, Moskát C, Barta Z, Hauber ME. 2013 Simultaneous viewing of own and parasitic eggs is not required for egg rejection by a cuckoo host. *Behav. Ecol.* **24**, 1014–1021. (doi:10.1093/beheco/art004)
70. Langmore NE, Stevens M, Maurer G, Kilner RM. 2009 Are dark cuckoo eggs cryptic in host nests? *Anim. Behav.* **78**, 461–468. (doi:10.1016/j.anbehav.2009.06.003)
71. Thomas M, Moskát C, Hauber ME. 2017 Cognitive decision rules for egg rejection. In *Avian brood parasitism: behaviour, ecology, evolution and coevolution* (ed. M Soler), pp. 437–448. Cham, Switzerland: Springer International Publishing.
72. Canniff L, Dainson M, López AV, Hauber ME, Grim T, Samaš P, Hanley D. 2018 Probing the limits of egg recognition using egg rejection experiments along phenotypic gradients. *J. Vis. Exp*. **22**, 138. (doi:10.3791/57512)
73. Troscianko J, Wilson-Aggarwal J, Stevens M, Spottiswoode CN. 2016 Camouflage predicts survival in ground-nesting birds. *Sci. Rep.* **6**, 19966. (doi:10.1038/srep19966)
74. Scardamaglia RC, Reboreda JC. 2014 Ranging behavior of female and male shiny cowbirds and screaming cowbirds while searching for host nests. *Auk* **131**, 610–618. (doi:10.1642/AUK-14-54.1)
75. Fiorini VD, Reboreda JC. 2006 Cues used by shiny cowbirds (*Molothrus bonariensis*) to locate and parasitise chalk-browed mockingbird (*Mimus saturninus*) nests. *Behav. Ecol. Sociobiol.* **60**, 379–385. (doi:10.1007/s00265-006-0175-3)
76. Stevens M, Troscianko J, Spottiswoode CN. 2013 Repeated targeting of the same hosts by a brood parasite compromises host egg rejection. *Nat. Commun.* **4**, 1–6. (doi:10.1038/ncomms3475)
77. Moskát C, Hauber ME, Avilés JM, Bán M, Hargitai R, Honza M. 2009 Increased host tolerance of multiple cuckoo eggs leads to higher fledging success of the brood parasite. *Anim. Behav.* **77**, 1281–1290. (doi:10.1016/j.anbehav.2009.01.030)
78. De La Colina MA, Mahler B, Reboreda JC. 2011 Differences in morphology and colour pattern of shiny cowbird (*Molothrus bonariensis*) eggs found in nests of two hosts. *Biol. J. Linn. Soc.* **102**, 838–845. (doi:10.1111/j.1095-8312.2011.01605.x)
79. Caves EM, Green PA, Zipple MN, Peters S, Johnsen S, Nowicki S. 2018 Categorical perception of colour signals in a songbird. *Nature* **560**, 365–367. (doi:10.1038/s41586-018-0377-7)
80. Benard J, Stach S, Giurfa M. 2006 Categorization of visual stimuli in the honeybee *Apis mellifera*. *Anim. Cogn.* **9**, 257–270. (doi:10.1007/s10071-006-0032-9)
81. Cropper SJ, Kvansakul JGS, Little DR. 2013 The categorisation of non-categorical colours: a novel paradigm in colour perception. *PLoS ONE* **8**, e59945. (doi:10.1371/journal.pone.0059945)
82. Harnad S. 1987 Psychophysical and cognitive aspects of categorical perception: a critical overview. In *Categorical perception: the groundwork of cognition* (ed. S Harnad), pp. 1–25. New York, NY: Cambridge University Press.
83. Dukas R, Nickolas MW. 1994 Categorization of food types enhances foraging performance of bumblebees. *Anim. Behav.* **48**, 1001–1006. (doi:10.1006/anbe.1994.1332)