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The modelling of avian visual perception predicts behavioural rejection responses to foreign egg colours

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How do birds tell the colours of their own and foreign eggs apart? We demonstrate that perceptual modelling of avian visual discrimination can predict behavioural rejection responses to foreign eggs in the nest of wild birds. We use a photoreceptor noise-limited colour opponent model of visual perception to evaluate its accuracy as a predictor of behavioural rates of experimental egg discrimination in the song thrush *Turdus philomelos*. The visual modelling of experimental and natural eggshell colours suggests that photon capture from the ultraviolet and short wavelength-sensitive cones elicits egg rejection decisions in song thrushes, while inter-clutch variation of egg coloration provides sufficient contrasts for detecting conspecific parasitism in this species. Biologically realistic sensory models provide an important tool for relating variability of behavioural responses to perceived phenotypic variation.

Keywords: birds; brood parasitism; egg rejection; eggshell colour; visual perception

1. INTRODUCTION

Avian and human colour vision are dramatically different (Bennett & Théry 2007). The application of portable spectrophotometers to measure reflectance spectra over the full avian visible range (i.e. 300–700 nm) has considerably increased our ability to distinguish and characterize different signals of phenotypic coloration in birds. Representative studies include adult plumage (Cuthill *et al.* 1999), eggshells (Cherry & Bennett 2001) and nestling gapes (Hunt *et al.* 2003). Yet, physical reflectance measurements do not account for how avian sensory systems actually process and discriminate reflected light (Endler 1990; Bennett & Théry 2007). To understand the mechanisms involved in driving the evolution of avian colours, including the immense variability in eggshell coloration and maculation (Wallace 1889), it is essential to assess how biologically or functionally relevant physical

(reflectance-based) indices of coloration relate to the limits of avian sensory perception and predict behavioural responses.

Song thrushes, *Turdus philomelos*, are occasionally impacted by intraspecific brood parasitism (Grim & Honza 2001) and serve as rare but suitable hosts of costly interspecific parasitism by common cuckoos *Cuculus canorus* (Grim 2006). Increased behavioural decision rates to reject foreign eggs for incubation by song thrushes were previously related to human-perceived (Davies & Brooke 1989; Grim & Honza 2001) or physical measures of colour mismatch (Honza *et al.* 2007) between experimental eggs and females' own eggs. We subsequently assessed the relationship between visual models of discrimination and behavioural measures of rejection responses of nesting wild song thrushes in response to experimental eggs of diverse colours (Honza *et al.* 2007). Average rejection rates in response to experimentally introduced song thrush eggs are also variable between geographical regions (lower in Europe (Davies & Brooke 1989; Honza *et al.* 2007) and higher in the introduced range of New Zealand (Hale & Briskie 2007)). Thus, we compared discriminability of conspecific eggs from different females in the Czech Republic with a much larger dataset of intraspecific comparisons from New Zealand field data. We predicted that the average discriminability of song thrush eggshell colours between different clutches would be greater than that for two eggs from the same clutch.

2. MATERIAL AND METHODS

We used published data from song thrushes on the spectral reflectance of painted plaster or real conspecific eggs and behavioural rejection responses, following the experimental introduction of these eggs into wild clutches in the Czech Republic (for detailed methods, see Honza *et al.* 2007). Rejection included both egg ejection and nest desertion, as these are specific responses to experimental brood parasitism in the song thrush (Grim & Honza 2001).

In 2004–2005, we collected a single egg from 102 song thrush clutches (and a second egg from 40 clutches) within its introduced range in New Zealand (for study site, spectrophotometry methods and natural variability in song thrush eggshell colours, see Cassey *et al.* (in press)), to assess the relative differences in discriminability between conspecific eggshell colours from different clutches and eggs within the same clutch.

We applied a photoreceptor noise-limited colour opponent model (Kelber *et al.* 2003; Endler & Mielke 2005) that estimates the difference between two colours with respect to the spectral sensitivities of all four avian single cone photoreceptors (ultraviolet, short wavelength, medium wavelength and long wavelength) corrected for the receptor noise in each cone (Vorobyev & Osorio 1998). The units for perceptual differences (Δ_e) between two spectra are just-noticeable differences (JNDs), such that 1 JND represents the threshold of possible discrimination. As JND increases, the discrimination of two colours is predicted to increase rapidly and can take place under more unfavourable viewing conditions (Vorobyev & Osorio 1998).

Relative sensitivities of the four photoreceptors were kindly provided by Nathan Hart for the congeneric European blackbird *Turdus merula* (see Hart *et al.* (2000) for microspectrophotometric results). Predicted spectral sensitivities were calculated using the analytical expressions provided for the spectra of visual pigments and oil droplets (Govardovskii *et al.* 2000; Hart & Vorobyev 2005). We used the effect of woodland 'canopy-filtered green light' as ambient irradiance in these models (Endler 1993).

Visual models were constructed in the SAS (v. 8.02) interactive matrix language (PROC IML). Logistic regression models (PROC LOGISTIC) were built to assess whether increases in observed rejection behaviour were associated with the average difference in receptor quantum catches between conspecific ($q_i(\text{conspecific}_j)$) and experimental ($q_i(\text{artificial}_j)$) eggs, where q_i is the relative quantum catch of receptor i , normalized and adapted to its irradiance (Vorobyev *et al.* 1998), and larger values indicate relatively greater stimulation of the photoreceptors. For each of the 10 artificial egg

Table 1. Model estimates (slopes) from logistic regression that assesses the relationship between frequency of experimental egg rejection and the average differences between conspecific and artificial model eggs in receptor quantum catches for the four avian single cones (Hart 2001). ΔAIC_i is the difference in AICc values (corrected for small sample size bias) between each individual model and the best candidate model from this dataset. The weight (w_i) for each model is the likelihood that the single model with the lowest AICc is the best explanatory model for this dataset. Only models with $w_i > 0.01$ are included.

	UV (ultraviolet)	S (short wavelength)	M (medium wavelength)	L (long wavelength)	ΔAIC_i	w_i
	estimate (s.e.)	estimate (s.e.)	estimate (s.e.)	estimate (s.e.)		
UV+S	-47.65 (10.84)	12.48 (3.12)			0.00	0.54
S+M+L		55.66 (14.15)	45.30 (10.81)	44.00 (11.16)	1.09	0.11
UV+S+M	-44.00 (11.16)	11.66 (2.13)	1.30 (1.39)		1.09	0.11
UV+S+L	-45.29 (10.81)	10.36 (3.73)		-1.30 (1.39)	1.09	0.11
UV+M+L	-55.65 (14.15)		-10.36 (3.73)	-11.66 (3.13)	1.10	0.11

types of Honza *et al.* (2007), the averages were calculated across 25 pairwise comparisons for the replicate conspecific ($j=1-5$) and artificial ($k=1-5$) eggshell reflectance spectra. We constructed candidate models (table 1) using all possible subsets of our global model and compared them based on the Akaike information criterion (Burnham & Anderson 2002). Predicted rejection behaviour values from the best model were compared with the observed rates of rejection behaviour using correlation statistics.

3. RESULTS

The average discriminability between natural conspecific song thrush eggs in the Czech Republic, Δ_e (\pm s.d.) was 1.63 JND (\pm 0.67). The average discriminability of eggshell colours, Δ_e (\pm s.d.) from natural conspecific eggs compared with experimentally painted eggs ranged from 7.83 (\pm 0.89) to 63.89 JND (\pm 3.86). The greatest difference in perceived colours of two song thrush eggs from natural nests in New Zealand was 4.04 JND. As predicted, the average discriminability of song thrush eggshell colours between different clutches (average $\Delta_e \pm$ s.e. = 1.06 ± 0.63 JND) was significantly greater than that of eggs from the same clutch (average $\Delta_e \pm$ s.e. = 0.83 ± 0.50 JND) ($t=2.97$, $n=102$ clutches, $p < 0.001$).

In a logistic regression analysis, the best model describing the average rejection rate of artificial eggs included terms for both ultraviolet and short wavelength-sensitive photon capture (table 1). The difference in ultraviolet photon capture was the only term for which the model-averaged estimate did not include zero (estimate (95% CI) = -42.23 (-79.35 , -5.1083)). The predicted estimates of rejection rate back calculated from the best model (table 1) correlated well with the observed rejection rates (Pearson's $r=0.86$, $n=10$, $p=0.001$), with the notable exception of 'orange'-type experimental eggs (figure 1).

4. DISCUSSION

Prior work showed a match between avian perceptual modelling and behavioural responses to colour variation in both the laboratory (e.g. operant training (Goldsmith & Butler 2005)) and the field (e.g. mate choice (Loyau *et al.* 2007), foraging (Schaefer *et al.* 2007)). We provide the first test of the functional relationship between predicted discrimination and behavioural variation in egg rejection responses in wild birds. Specifically, perceptual modelling of egg colours identified that average rejection rates of

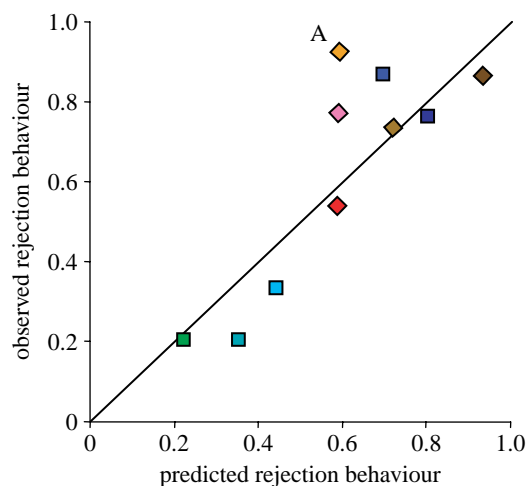


Figure 1. Bivariate scatter plot for observed rejection rates (frequency of ejection and nest desertion combined) of experimental eggs from song thrush nests against predicted rejection rates (p_i) for the model: $\text{logit}(p_i) = -1.96 - 47.65 \text{DIFF}(\text{UV}) + 12.48 \text{DIFF}(\text{SWS})$ in table 1. Behavioural rates and coloured loci correspond to the human-perceived mimetic (square loci) and non-mimetic (diamond loci) experimental colours from Honza *et al.* (2007). The 1:1 line is depicted. The loci A is the 'orange'-type artificial egg discussed in the text.

experimental eggs increased as the difference between ultraviolet components (negative estimate) and short wavelength components (positive estimate) increased between experimental and conspecific eggs (table 1). Thus, we confirm an avian-specific perceptual role of these colour components in influencing behavioural decision rules in song thrushes (Honza *et al.* 2007).

Our models also demonstrate that, despite very high predicted discriminability of painted eggs from conspecific eggs, the proportion of foreign eggs accepted in the Czech Republic was always greater than zero. In fact, the average discriminability Δ_e (log transformed) was not associated with the rejection responses among wild song thrushes (logistic regression; estimate \pm s.e. = 0.002 ± 0.011 , Wald $\chi^2 = 0.05$, $p=0.823$). Instead, observed egg rejection rates were best predicted by perceptual differences between conspecific and artificial eggs from just two receptors: the ultraviolet and short wavelength (table 1; figure 1).

Several ecological, geographical, developmental and species-specific differences are known to modulate

acceptance and rejection behaviours of individuals (Davies 2000). These behaviours include the costs of damaging a females' own eggs during ejection of foreign eggs (Moskát & Hauber 2007), ontogenetic and physical constraints to identify and grasp foreign eggs (Hoover et al. 2006), and social retaliation by parasites against rejector hosts (Hoover & Robinson 2007). Incorporating these contexts into sensory models may provide the most interesting research avenues for explaining additional components of the mismatch between the predicted levels of perceptual discrimination and the observed behavioural decisions to reject foreign eggs.

Our study was conducted on private land with the express permission of the landowners and followed institutional and governmental permits as required by the New Zealand Department of Conservation.

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