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Different recognition cues reveal the decision rules used for egg rejection by hosts of a variably mimetic avian brood parasite

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Abstract Brood parasitism imposes several fitness costs on the host species. To reduce these costs, hosts of avian brood parasites have evolved various defenses, of which egg rejection is the most prevalent. In the face of variable host-parasite mimicry and the costs of egg discrimination itself, many hosts reject only some foreign eggs. Here, we experimentally varied the recognition cues to study the underlying cognitive mechanisms used by the Chalk-browed Mockingbird (*Mimus saturninus*) to reject the white immaculate eggs laid by the parasitic Shiny Cowbird (*Molothrus bonariensis*). Immaculate eggs are the only parasite eggs rejected by this host, as it accepts all polymorphic, spotted eggs laid by cowbirds. Using a within-breeding pair experimental design, we tested for the salience of spotting, UV reflectance, and brightness in eliciting rejection. We found that the presence of spotting significantly decreased the probability of rejection while increments in brightness significantly increased rejection frequencies. The cognitive rules underlying mockingbird rejection behavior can be explained by a decision-making model which predicts changes in the levels of rejection in direct relation to the number of relevant attributes shared between host and parasite eggs.

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Introduction

Obligate avian brood parasites place their eggs in nests of other species, which perform all aspects of parental care from incubation to past fledging (Davies 2000). Raising parasite offspring imposes fitness costs on these hosts as the survival of own eggs and chicks drops significantly in parasitized broods (Øien et al. 1998; Payne and Payne 1998; Hauber 2002, 2003; Hoover 2003; Reboreda et al. 2003). As a consequence, co-evolutionary interactions have resulted in hosts evolving antiparasite defenses (Rothstein and Robinson 1998; Schulze-Hagen et al. 2009; Davies 2011; Kilner and Langmore 2011). In addition to aggression toward the adult parasite (Moksnes et al. 1991; Røskaft et al. 2002a; Fiorini et al. 2009) and the discrimination of parasitic chicks in the nest (Langmore et al. 2003; Schuetz 2005; Grim 2007; Tokue and Ueda 2010), by far the most prevalent and commonly documented defense is the rejection of foreign eggs (Rothstein 1990; Davies 2000, 2011; Peer and Sealy 2004; Kilner and Langmore 2011; Grim et al. 2011).

Although some species reject all foreign eggs (Vikan et al. 2009), others are imperfect rejecters or do not reject parasite eggs at all (Stokke et al. 2005; Moskát and Hauber 2007). In theory, a recognition threshold exists in all cognitive abilities to discriminate acceptable and non-acceptable phenotypes, which would determine the rejection decision used by the host against a distribution of self/foreign egg cue dissimilarity (called the conspecific acceptance threshold: Reeve 1989; McLean and Maloney 1998; Servedio and Lande 2003; Servedio and Hauber 2006). Experimental evidence collected from different hosts of brood parasitic birds

showed that egg cues leading to rejection are related to specific visual characteristics that depend not only on particular perception capabilities (Bowmaker et al. 1997; Holen and Johnstone 2004; Cassey et al. 2008; Safran and Vitousek 2008; Stoddard and Stevens 2010, 2011) but also on the ambient light characteristics determined by the habitat and the nest type (Avilés et al. 2005; Langmore et al. 2005; Honza et al. 2011). Hosts appear to use the most reliable available cues in making rejection decisions (Spottiswoode and Stevens 2010), and egg features that may be leading to rejection include size (Marchetti 2000), eggshell maculation (Lahti and Lahti 2002; López-de-Hierro and Moreno-Rueda 2010), total brightness (Lahti 2006), background color (Moskát et al. 2008), and ultraviolet (UV) reflectance (Honza et al. 2007; Honza and Polačiková 2008; but see Avilés et al. 2006), although hosts may also integrate several different egg characteristics (Rothstein 1982; Spottiswoode and Stevens 2010). Discrimination may rely on the presence of these cues over the entire eggshell or at a specific region of the egg (Polačiková and Grim 2010; Polačiková et al. 2011). Context-dependent shifts of the acceptance threshold are prevalent among some egg rejecter hosts of avian brood parasites (e.g., Lindholm 2000; Hauber et al. 2006; but see Vikan et al. 2009), implying that rejection behavior can be plastic and that it is not strict limitations in perceptual discrimination which govern acceptance or rejection decisions.

The aim of this study was to test the specific and relative role of visible phenotypic cues used to recognize parasite eggs by the Chalked-browed Mockingbird (*Mimus saturninus*) (hereafter mockingbird). This species is one of the main hosts used by the obligate brood parasitic Shiny Cowbird (*Molothrus bonariensis*) (hereafter cowbird) in Argentina (De Mársico et al. 2010). The Shiny Cowbird is a highly generalist brood parasite that uses over 250 bird species throughout its distribution in the Americas (Lowther 2011). While some cowbird victims reject most parasite eggs (Mason 1986), others are accepters and do not reject any parasite eggs at all, and still another group of host species, including the mockingbird, comprises partial or intermediate rejecters. From the highly polymorphic egg types laid by different female cowbirds (Hudson 1874; Friedmann 1929; Mahler et al. 2008; de la Colina et al. 2011), mockingbirds accept all spotted eggs but reject the white immaculate cowbird eggs (Fraga 1985; Mason 1986; Sackmann and Reboreda 2003). This partial (or intermediate, sensu Røskaft et al. 2002b; Moskát et al. 2010; Samaš et al. 2011) rejection behavior allows us to test which of the attributes of the parasite egg elicit foreign egg rejection in this host. Here, we studied how spotting, UV reflectance, and total brightness affected the probability of egg rejection by mockingbirds. Between-subject designs, as used in several previous studies, cannot reveal whether population-level variation in rejection responses reflects

variation within individuals (flexible individual tactics), between individuals (fixed individual strategies), or both (sensu Gross 1996; Samaš et al. 2011). As our study is the first to experimentally test the cues used for egg rejection in a host species using a within-breeding pair design, we are in the position to assess and account for the variation among individuals in the response to diverse foreign eggs.

Different cognitive mechanisms have been proposed to guide the decision rules regarding foreign egg recognition. Rejection might be based on discordance, where the host assesses differences between egg phenotypes within the same clutch, or on recognition from a template, where the host rejects on the basis of an innate or learned recognition template (Rothstein 1974; Moskát et al. 2010) against which it detects dissimilar eggs (Avilés et al. 2010). Here, we studied whether dissimilarities leading to rejection are based on one particular cue or on a combination of several different cues that have either equal or different weights in eliciting rejection. To this end, a decision-making mechanism, that has been useful to understand food preferences in birds (Pompilio and Kacelnik 2010), was employed to explain how the host evaluates different egg attributes in order to accept or reject a parasite (or experimental) egg. The original model (Dominance-Valuing Model: Wedell 1991) proposes that subjects compare simultaneously any single attribute and then prefer the options which have advantages in most attributes (the model allows the subject to assign either equal or different weight to each attribute). In the context of brood parasitism, the preferred option for the host can be defined in relation to the similarity with its own eggs. The experimental eggs comprising each treatment differ from host eggs in a number of shared attributes. The model predicts no rejection for eggs that are equal in all of the relevant attributes, rejection when none of the relevant dimensions are equal, and partial rejection for eggs that are different in some aspects but equal in others. The findings of this study have relevance for understanding and predicting the course of behavioral and phenotypic evolution; specifically it addresses the question of whether co-evolutionary interactions between hosts and parasites progress through arms races in single perceptual domains (e.g., spotting, brightness), or multiple visual cues combine to influence the evolution of acceptance thresholds and the types of host-parasite perceptual mimicry (Rothstein 1982).

Materials and methods

Study site

Experiments were carried out at "Reserva el Destino," near the town of Magdalena (35°8′S, 57°23′W), Buenos Aires Province, Argentina, during the austral reproductive

seasons (October–January) 2008–2009 and 2009–2010. Natural parasitism rate of mockingbird nests in this area is 66 % (Fiorini and Reboreda 2006). In an area of 67 ha, we searched for breeding pairs by focusing on mockingbird activity and then inspecting potential nesting sites within the territory of the pair. Mockingbirds build open nests in shrubs or trees with dense foliage at a height of 1.5–2.5 m. The nest is a large open cup of twigs (outer diameter 20–25 cm) lined with fibers and horsehair, with a clutch size ranging from 3 to 5 (Fiorini and Reboreda 2006). Eggs are 28.6 ± 0.3 mm (mean ± SE) in length and 20.4 ± 0.2 mm in width and are maculated on a greenish background (Fiorini and Reboreda 2006). We captured and individually color-banded 25 breeding pairs and followed their breeding attempts until experiments were completed. For eight of these pairs, we could not fully complete the experiments due to predation or nest abandonment.

Experimental egg design

Shiny cowbirds lay spotted or immaculate white eggs. We compared color and morphometric variables between both egg morphs in order to determine the specific attributes that differ between them and might be used by mockingbirds as cues for rejection (Table 1). Color variables were calculated using reflectance spectrometry (see below) and morphometric measures (length and width) were taken with a calliper to the nearest 0.1 mm. Volume was calculated as length $\times$ width^2 $\times$ 0.515 (Nolan and Thompson 1978). Table 1 shows ranges for color and morphometric variables measured on natural immaculate and spotted cowbird eggs. We found that ranges did not overlap for following variables: total brightness, UV chroma, blue chroma, and red chroma. However, ranges of blue chroma are virtually continuous and

we thus dismissed this variable as a possible cue used by mockingbirds for rejection. Red chroma, on the other hand, reflects the difference between both egg morphs in the presence of spots. Spotted eggs show the typical reflectance peaks of porphyrins in the red segment of the spectrum (Igic et al. 2011), which are absent in immaculate eggs (Fig. 1). Thus, we designed our experimental eggs to study the effects of spotting, UV reflectance, and total brightness on mockingbird rejection behavior.

Experimental eggs were made of plaster of Paris, with dimensions of a mean shiny cowbird egg (24.9 mm $\times$ 18.8 mm; de la Colina et al. 2011). All eggs were covered with matte water-based varnish after the pattern of each experimental treatment (Table 2) was applied, in order to protect the model surface and appearance from weathering. Spotting and UV reflectance were tested separately in pair-wise experiments. Egg pair 1) Spots: Sp+/Sp−, present/absent (similar brightness and absence of UV reflectance, Table 2). Spotted eggs (Sp+) were created by applying brown ink with a tooth brush over the white eggs; eggs without spots (Sp−) were painted with the same brown color mixed with white ink, creating a uniformly beige-colored egg. Egg pair 2) UV reflectance: UV+/UV− (similar brightness and absence of spots, Table 2). UV+ eggs were plaster eggs covered with white Teflon tape (Dupont ®); UV− were plaster eggs painted with white ink.

Egg pair 1 had greater brightness than egg pair 2 (Table 2, Fig. 1), and experimental eggs within each egg pair had similar brightness values (Table 2, Fig. 1). To test for rejection in response to brightness differences, we compared between egg pairs (see below). We quantified the brightness of the eggs by measuring reflectance using an Ocean Optics 2000 Spectrometer (Ocean Optics, Inc.,

Table 1 Comparison between natural immaculate and spotted cowbird eggs

	Natural immaculate cowbird egg (N = 6)	Natural spotted cowbird egg (N = 6)
Brightness[a] (total reflectance)	7707–8559	4138–6232
UV chroma[a]	0.134–0.139	0.100–0.126
Blue chroma[a]	0.190–0.195	0.168–0.189
Green chroma	0.212–0.215	0.187–0.214
Yellow chroma	0.227–0.231	0.230–0.246
Red chroma[a]	0.225–0.230	0.245–0.293
Length (cm)	2.18–2.49	2.24–2.38
Width (cm)	1.84–1.90	1.88–2.00
Volume (cm^3)	3.93–4.63	4.22–4.74

Ranges for coloration and morphometric variables are shown. [a] non-overlapping ranges between egg morphs. For measurement procedures see text
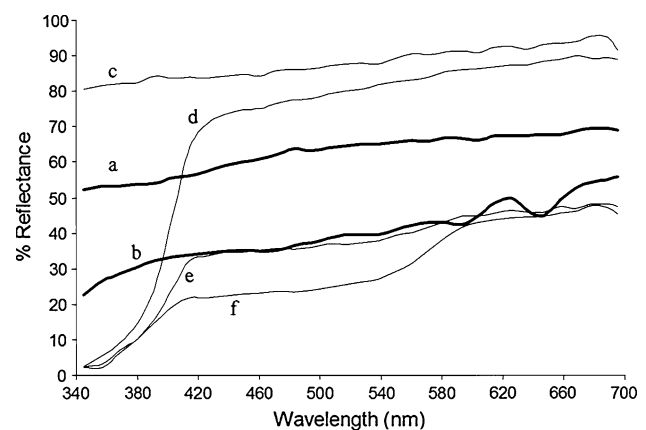

Fig. 1 Average reflectance spectra of natural shiny cowbird and experimental eggs. *a* Natural cowbird immaculate egg (N = 3); *b* natural cowbird spotted egg (N = 5); *c* experimental UV+ egg (N = 3); *d* experimental UV− egg (N = 2); *e* experimental spotted Sp+ egg (N = 4); *f* experimental uniformly beige Sp− egg (N = 2)

Table 2 Attributes of mockingbird eggs and experimental eggs tested for rejection behavior in this host

Egg pair	Name of the egg (treatment)	UV	Spots	Brightness	Brightness (total reflectance)	UV chroma $(R_{340-400}/R_{340-700})$
1	UV+ (teflon cover)	+	−	+	11190–11590	0.151–0.153
	UV− (white ink)	−	−	+	8169–9009	0.029–0.137
2	Sp+ (brown spots)	−	+	−	4373–6528	0.039–0.090
	Sp− (uniform beige ink)	−	−	−	3814–5076	0.032–0.044
	Mockingbird egg	−	+	−	1586–3814	0.065–0.084

UV+/− represents greater/lower levels of UV reflectance (UV chroma); Spots+/− represents presence/absence of spots; Brightness+/− represents greater/lower levels of brightness (total reflectance). The last two columns show the ranges of the experimental and host eggs for brightness and UV chroma

Dunedin, Florida, USA) with a PX-2 pulsed xenon light source (220–750 nm). Measurements were taken at a 90° angle from a 6-mm-diameter area. Reflectance was recorded each 0.35 nm within the avian visible spectrum from 340 to 700 nm using OOIBASE32 software and expressed relative to a white reflection standard of barium sulfate, following Osorio and Ham (2002). We performed three measurements at haphazard sites on each egg and took median reflectance values for 3 nm bins for each measurement. Reflectance values below 340 nm were excluded because of considerable noise at these wavelengths. For each egg, we calculated the average reflectance and a brightness score as the sum of all reflectance values. We also calculated values of reflectance ratios as estimates of chroma values for different segments of the reflectance spectrum (Honza et al. 2007): UV chroma: $R_{340-400/340-700}$; blue chroma: $R_{400-475/340-700}$; green chroma: $R_{475-550/340-700}$; yellow chroma: $R_{550-625/340-700}$; and red chroma $R_{625-700/340-700}$.

Experimental design

Each breeding pair was exposed to one experimental egg pair sequentially in a breeding attempt and to the other experimental egg pair in a subsequent breeding attempt. The design was balanced for experimental egg pair with approximately half of the breeding pairs receiving as first treatment Sp+/Sp− and the remaining ones UV+/UV−. Within experimental egg pairs, the order of presentations was balanced for egg type. We placed the experimental egg in the mockingbird nest after their first or second egg was laid. We left the egg in the nest for 48 h and recorded whether it was accepted or rejected after that period of time (mockingbirds reject immaculate shiny cowbird eggs within the first 24 h after parasitism, Fraga 1985; Sackmann and Reboreda 2003). The first experimental egg was then replaced by the second one, which was also left in the nest for 48 h when acceptance or rejection was recorded. The second experimental egg was removed if not rejected and breeding pairs were not further disturbed during that breeding attempt. Experimental addition of eggs during

mockingbird laying reflects a natural context of parasitism, as cowbirds synchronize laying with their host (Fiorini and Reboreda 2006) and do not remove its eggs (Sackmann and Reboreda 2003).

The second egg pair was placed in the same way at a subsequent breeding attempt of the same mockingbird pair. Abandoned nests ($N = 8$) were excluded from the analysis since it was not possible to determine if desertion was a consequence of experimental parasitism. To test for the effect of brightness on egg rejection, we compared Sp− and UV− experimental eggs (both with absence of spots and absence of UV reflectance).

Statistical analysis

We were primarily interested in the effects of spotting, UV reflectance, and brightness on host rejection behavior. We also included factors in the analysis that may potentially affect host behavior. To that end, data were clustered by breeding pairs (tested repeatedly), breeding attempt (two egg models introduced shortly after each other within one breeding attempt), order of the eggs (first or second, nested within breeding attempts), year (the data were collected in two consecutive breeding seasons), and date (centered by year), since some pairs were tested earlier in the season and others later. We analyzed our experimental data using generalized linear mixed models (GLMM). The full model contained the following explanatory variables: (i) fixed effects of "spotting" (nominal: Sp+ and Sp−), (ii) fixed effects of "UV reflectance" (nominal: UV+ and UV−), (iii) fixed effects of "brightness" (nominal: B+ and B−), (iv) random effects of "breeding pairs," (v) fixed effects of "breeding attempt" (nominal: first and second), (vi) fixed effects of "order of the eggs" (nominal: first and second; nested within "breeding attempt"), (vii) fixed effects of "year" (nominal: first and second), and (viii) "date" (continuous, centered by "year"). We followed backward elimination of non-significant terms (including all covariates and the relevant interactions) in order to remove the non-significant predictors and produce the minimum

adequate model. In each iteration, we eliminated the covariate with the highest p value, conditional on being greater than 0.10. The dependent variable was host response to experimental eggs (nominal: accepted vs. rejected). Even though the use of logit is recommended for binomial distributions of the error term, it was not possible to apply such a procedure to our data sample because one of the factors (spotting) predicts rejection behavior with probability 1. Under such circumstances the coefficient takes an infinite value, meaning that it is not possible to generate estimates. For this reason, the response variable was analyzed following a linear model. This procedure generates unbiased estimates under controlled experimental designs since the error term does not correlate with the estimated coefficients. We fitted all models in STATA (Data Analysis and Statistical Software, StataCorp LP).

Results

Approximately half of the mockingbird breeding pairs (45 %) rejected the uniformly beige-colored egg, whereas none of them rejected the spotted egg ($N = 20$) (Fig. 2). White eggs were rejected by most mockingbird pairs (UV− eggs: 73 %, UV+ eggs: 86 %, $N = 22$) (Fig. 2). Rejection rates are close to those reported for natural cowbird eggs (spotted: 17 and 0 %; immaculate: 100 %; Fraga 1985; Sackmann and Reboreda 2003, respectively) (Fig. 2).

Regression analyses of spotting, brightness (and its interaction with breeding attempt), and year explained 52 % of the variation in the rejection behavior of mockingbirds ($F_{4, 79} = 19.24$, $p < 0.001$). The presence of spots on the experimental eggs significantly decreased the probability of rejection (Table 3). In fact, none of the breeding pairs rejected spotted eggs. On the other hand, increments of brightness significantly increased the probability of rejection. This effect was smaller during the second breeding attempt (Table 3). As shown in Table 4, six breeding pairs (35 %) exclusively rejected B+ eggs while two breeding pairs (12 %) exclusively rejected B− eggs. Of the remaining breeding pairs, five (29 %) rejected both B+ and B− eggs and four (24 %) accepted both. "Year" did not significantly affect rejection behavior (Table 3).

UV reflectance did not significantly affect rejection behavior (this factor was excluded from the final model as a result of backward elimination). As shown in Table 4, only three breeding pairs (13.5 %) exclusively rejected the UV+ egg while none rejected the UV− egg only. Of the remaining breeding pairs, sixteen rejected both UV+ and UV− eggs (73 %) and three (13.5 %) accepted both.

Table 5 shows how the attributes of the experimental eggs overlap with the attributes of host eggs and the percentage of mockingbird rejection for each one. Spotted (Sp+) experimental eggs do not differ from mockingbird eggs (Table 2), sharing the presence of spots and reduced levels of brightness and UV reflectance. Uniformly beige-colored (Sp−) experimental eggs retain low levels of brightness and UV, but lack the spots, whereas UV− eggs increase in brightness sharing only the absence of UV with the host's eggs. Finally, UV+ eggs do not share any of the attributes with mockingbird eggs. The percentage of rejection for each experimental egg (rejecting/total breeding pairs) increases with the number of different attributes between experimental and host eggs.

Discussion

The probability of mockingbirds rejecting a foreign egg can be best explained by the following attributes: spotting and brightness. Rejection sharply decreased with the presence of spots and increased with greater levels of brightness.

The presence of spots is an accurate predictor of the acceptance of the brood parasite's egg by this host. This raises the question whether these hosts accept spotted cowbird eggs because spotting is a necessary condition (i.e., spotted eggs are similar to host's own eggs not only in maculation but also in other relevant attributes such as brightness, UV reflectance, and shape (de la Colina et al. 2011)) or because spotting is a necessary and sufficient condition (being spotted is enough for acceptance). Critically, we demonstrate that whereas spotting leads to full acceptance of foreign eggs, the absence of spotting does not necessarily lead to full rejection since half of Sp− (uniformly beige-colored) eggs are accepted. These results suggest that a complex decision-making mechanism is used by this species to recognize and reject foreign eggs. In fact, the results confirm that increments in brightness increased the probability of rejection. Strikingly, during the second breeding attempt, mockingbirds seem to be less tolerant to brightness. Perhaps this increment in the rejection behavior to B+ eggs can be explained by experience and/or specifically by learning (Lotem 1993).

The results obtained in this study are compatible with the logic of the Dominance-Valuing Model (Wedell 1991), because the percentage of rejection increases with any increment in the differences of the eggs' attributes. Accordingly, when we compare the number of visible attributes in which the experimental eggs differ from host eggs (see Table 5), it becomes clear that the level of rejection increases when host and experimental eggs are more dissimilar: no rejection is observed when the 3 manipulated attributes are similar (spotted egg), partial

Fig. 2 Comparison of mockingbird rejection frequencies in manipulations with sequential presentation of pairs of experimental eggs that varied in a single phenotypic attribute: Spotting (Sp+/Sp−), UV reflectance (UV+/UV−), and brightness (B+/B−). Eggs differing in brightness were represented by white (UV−) and uniformly beige-colored (Sp−) eggs. The last two columns show mockingbird average rejection frequencies of natural cowbird eggs (Fraga 1985; Sackmann and Reboreda 2003)
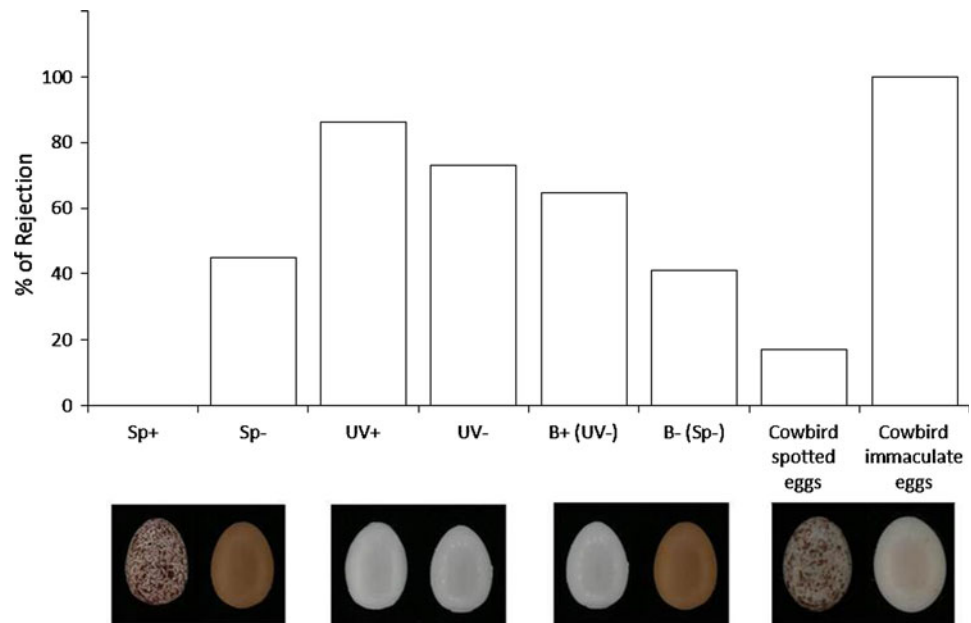

Table 3 Estimates of parameters and statistical significance of the final model ($N = 25$ pairs)

Factors	Estimate ± SE	p
Spotting	−0.45 ± 0.11	0.000
Brightness	0.87 ± 0.22	0.000
Breeding attempt * brightness	−0.45 ± 0.18	0.009
Year	0.17 ± 0.10	0.077

The model predicts the probability of the experimental egg's rejection

Table 4 Number of breeding pairs that accepted or rejected one or both eggs comprising each experimental pair of eggs varying in a single phenotypic attribute: spotting (Sp+/Sp−), UV reflectance (UV+/UV−), and brightness (B+/B−)

	Attribute	Reject only one	Reject both	Accept both
Egg pair 1	Sp+	0	0	11
	Sp−	9		
Egg pair 2	UV+	3	16	3
	UV−	0		
Post hoc comparison	B+ (UV−)	6	5	4
	B− (Sp−)	2		

rejection is observed when 2 attributes (brightness and UV reflectance) are similar (uniformly beige egg), the level of rejection increases when only 1 attribute (UV reflectance) is similar (white UV− egg), and the maximum level of rejection is observed when the eggs differ in all of the studied attributes (white UV+ egg). Although percentage of rejection slightly increases with the presence of UV reflectance, the results were not statistically significant for this attribute.

Mockingbirds do not reject experimental spotted eggs. However, when only the spots are eliminated, the percentage of rejection increases to almost 50 % (Table 5). This is the greatest change caused by the experimental manipulation of egg phenotype in this hosts' rejection behavior frequency. Following the same reasoning, notice that by increasing brightness (but not UV reflectance) the percentage of rejection increases from 45 to 73 %, whereas by adding a tertiary cue, UV reflectance, the percentage of rejection only increased rejection from 73 to 86 %. This observation is compatible with the idea that spotting has the largest weight in the cognitive decision rules of this host to reject foreign eggs, followed by brightness, and then, possibly, by UV reflectance. This qualitative analysis, however, has to be taken as preliminary, since the results presented in the table are not adjusted to repeated samples of the same breeding pair. The statistical analysis confirms the significance of spotting and brightness but not of UV reflectance, suggesting that at least two manipulated attributes play a role in the decision-making process. This multi-cue decision-making process might be also influenced by a perceptual polymorphism and/or cognitive variance in acceptance thresholds between individuals which results in the rejection of fewer eggs than those which are recognized as distinctly foreign (Antonov et al. 2009; Moskát and Hauber 2007).

Is this potential decision-rule common in other host species of variably or poorly mimetic brood parasites? The American Robin (*Turdus migratorious*), for example, seems to apply a similar while still flexible decision-making rule in order to reject parasite eggs. This host species usually rejects eggs that differ in any two of three relevant parameters (size, color, and/or spots). Small egg size is,

Table 5 Comparison between the four experimental egg types and real mockingbird eggs (Sp+/B−/UV−) in relation to the overlap of egg attributes: "Yes" indicates a similar attribute; "No" indicates a difference in the attribute

Name of the egg/treatment	Experimental Egg attributes	Host egg attributes			Total number of attributes for which eggs differ	% Rejection
		Sp+	B−	UV−		
Sp+	Sp+/UV−/B−	Yes	Yes	Yes	0	0 (0/20)
Sp−	Sp−/UV−/B−	No	Yes	Yes	1	45 (9/20)
UV−	Sp−/UV−/B+	No	No	Yes	2	73 (16/22)
UV+	Sp−/UV+/B+	No	No	No	3	86 (19/22)

The penultimate column shows the number of different attributes between experimental and host eggs. The last column shows the percentage of rejection for each experimental egg (rejecting/total breeding pairs)

however, the most important parameter eliciting rapid rejections perhaps because differences in size can be detected by both visual and tactile perception (Rothstein 1982). Similarly, Village Weaverbirds (*Ploceus cucullatus*) can distinguish their eggs from foreign ones using color and spotting as both reliable cues. No interaction has been observed between these variables, indicating that the birds assess color and speckling independently (Lahti and Lahti 2002). Warbling Vireos (*Vireo gilvus*), on the other hand, eject foreign eggs based exclusively on one cue: spotting pattern. Accordingly, foreign eggs that differ in two parameters are not more likely to be ejected than those that differ in only that single parameter (Underwood and Sealy 2006).

Mockingbirds do not have physical constraints of gape and beak size for grasping and ejecting cowbird eggs, which sometimes is the case in smaller hosts (Antonov et al. 2009). Still, our experiments confirm that mockingbirds are only partial rejecters and use a rejection rule that is subject to error, since they accept spotted shiny cowbird eggs, which represent a high proportion of local egg phenotypes of this parasite (75 % in this area; Tuero et al. 2007). Furthermore, white immaculate eggs are fully absent in parts of the sympatric cowbird–mockingbird distribution (Mahler et al. 2008). This indicates that mockingbirds are not using a consistently reliable cue to differentiate between shiny cowbirds' and their own eggs. The decision-making process for rejecting foreign eggs used by mockingbirds, therefore, appears to rely primarily on the absence of spots but also on brightness and, to a lesser extent, UV reflectance. It is possible that, although not perfect, cues that elicit rejection are the ones that are more salient and easy to detect (having, thus, a better cost-benefit ratio or a lower cognitive processing cost; Lotem 1993). In addition, the rejection of shiny cowbird eggs by mockingbirds can be costly as it increases the risk of host egg loss during subsequent parasite attacks. In recent work, Gloag et al. (2012) have found that mockingbird eggs are more likely to escape punctures inflicted by shiny cowbird females when more cowbird eggs accompanied them in the clutch, which may reduce the benefit of rejecting

parasite eggs when multiple parasitism is common. It remains to be evaluated whether non-rejecter hosts of variably mimetic brood parasites do not consider some foreign eggs as unacceptable or they do recognize these eggs as foreign but act so as not to reject them to minimize recognition errors and rejection costs (Moskát and Hauber 2007). A decision-making mechanism that is based on the summation of different attributes will be favored as it decreases the errors in recognizing foreign eggs. This mechanism likely evolves in hosts that are faced with polymorphic parasite eggs, as is the case in mockingbirds, where there is no directional selection pressure favoring the recognition of one particular cue. Identifying differences in many attributes might allow the recognition of several polymorphic foreign eggs, thus improving the overall effectiveness of antiparasite defenses early during the egg-laying and incubation stages.

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