Original Article

Simultaneous viewing of own and parasitic eggs is not required for egg rejection by a cuckoo host

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Many hosts have evolved diverse cognitive mechanisms to recognize and reduce the cost of social parasitism. For example, great reed warblers *Acrocephalus arundinaceus* can accurately reject closely mimetic eggs of brood parasitic common cuckoos *Cuculus canorus*. Yet, these same hosts are less effective at identifying and rejecting parasitism when the clutch is parasitized by multiple cuckoo eggs, suggesting a role for discordancy (the rejection of the egg type in the minority of the clutch) and/or online self-referent phenotype matching (the simultaneous viewing of cuckoo and own eggs in the nest) to reject foreign eggs. We tested whether the presence of host's own eggs is required for the discrimination of foreign eggs by dyeing hosts' own eggs with one of several colors so that clutches contained *(a)* 1 dyed and 4 unmanipulated eggs, *(b)* 3 dyed and 2 unmanipulated eggs, or 5 eggs dyed either *(c1)* differently or *(c2)* similarly. Rejection rates of dyed eggs varied widely between different colors and were highest in treatment *(a)*, with 1 dyed egg, compared with treatments with the majority *(b)* or all *(c1 and c2)* dyed eggs. However, relative rejection rates of dyed eggs were also consistent among specific colors across treatments, including *(c1)* and *(c2)*, where no unmanipulated own eggs were available for viewing and irrespective of whether eggs were dyed all different colors *(c1)* or the same colors *(c2)*. We conclude that these hosts can rely on comparisons of foreign egg colors against an internal recognition template of acceptable (own) egg phenotypes.

Key words: brood parasitism, egg recognition, egg rejection, multiple parasitism, phenotype matching, recognition template. [Behav Ecol]

INTRODUCTION

Obligate social parasites, including brood parasitic ants, fishes, amphibians, and birds, introduce their offspring into the clutch or brood of other species and rely on host species to provide costly care for the parasitic young (Sato 1986; Davies et al. 1989; Brown et al. 2009). Avian brood parasitism exerts strong coevolutionary selective pressures (e.g., Rothstein 1990; Soler and Møller 1996; Antonov et al. 2010), inducing parasites to evolve morphological and behavioral adaptations to minimize detection by hosts. In turn, hosts can evolve sensory and cognitive antiparasite responses to recognize and reject foreign eggs (Krüger 2007; Spottiswoode and Stevens 2011). Extensive studies of these coevolutionary arms races have focused on the mimicry of host egg colors by brood parasitic birds and the increasingly complex sensory, cognitive, and behavioral responses of hosts to mimetic parasite eggs (reviewed in Davies 2000, 2011). Some avian brood parasites have begun to exploit novel host species that have not yet evolved antiparasite responses (Hauber et al. 2004), whereas other hosts can successfully prevent parasitic exploitation altogether (Lovászi and Moskát 2004). Yet, in other hosts, parasitic mimicry is so effective that hosts cannot discriminate foreign eggs or young from their own (Avilés 2008; Ranjard et al. 2010; Langmore et al. 2011). In most cases, however, the arms race is ongoing; only some parasitic attempts succeed against the imperfect defense portfolios of hosts (e.g., Johnson and Herbers 2006; Antonov et al. 2010; Martin et al. 2011).

Foreign egg discrimination is the most well-documented anti-parasite adaptation among avian hosts of brood parasites (Davies 2000, 2011) and has been extensively studied using experimental approaches in the context of host egg mimicry by the common cuckoo *Cuculus canorus* (hereafter referred as cuckoo; Payne 2005). Cuckoo eggs typically resemble host eggs both in color and pattern (Davies and Brooke 1988, 1989; Moksnes and Røskaft 1995). They occasionally match host eggs in size (Török et al. 2004), but not in shape (Bán et al. 2011) or thickness (Spottiswoode 2010; Igic et al. 2011). The cognitive basis of parasitic egg discrimination can include learned cues both from self-referenced and socially acquired templates of own versus parasitic eggs (Lotem et al. 1995; Moskát and Hauber 2007; Stokke et al. 2007), and chicks (Sato et al. 2010) and adult phenotypes (Hauber and Sherman 2001; Davies and Welbergen 2008). Typically, the discrimination between own and foreign eggs depends on perceivable differences in the appearances of eggshells within the parasitized clutch, as revealed by spectrophotometric studies (Cherry et al. 2007; Honza et al. 2007), and perceptual modeling approaches, which account for the specific visual physiology of cuckoo hosts (e.g., Avilés 2008; Cassey et al. 2008; Stoddard and Stevens 2010, 2011; Igic et al. 2012).

Some experimental pieces of evidence suggest that hosts do not need to view the maculation of their own eggs in order to reject foreign eggs (Moskát et al. 2010). Similarly, learning the overall appearance of the hosts' own eggs (i.e., both maculation and background color) may be involved in rejecting foreign eggs even in the absence of host eggs in the clutch (Lotem et al. 1995; Moskát and Hauber 2007; de la Colina et al. 2012). Here, we focus on the background coloration of host versus foreign eggs to examine whether viewing own eggs is required to recognize and reject foreign eggs from the nest.

Regarding the cognitive basis underlying foreign egg recognition, a recent analysis by Moskát et al. (2010) demonstrated that the great reed warbler *Acrocephalus arundinaceus*, a regular cuckoo host, relies on at least 2 different mechanisms for egg recognition. One of these is discordancy, where hosts reject those eggs whose phenotype is in the minority in the clutch (Rothstein 1974; Lyon 2007). Accordingly, 10% of great reed warblers ejected their own eggs when clutches contained 4 similar artificially maculated parasitic eggs and 1 own egg (Moskát et al. 2010). An alternative, but not mutually exclusive, cognitive process is online self-referencing (a subtype of "self-referencing" sensu Hauber and Sherman 2001), whereby birds simultaneously view eggs within a clutch, comparing each against their known own eggs. The host's own eggs are probably identified shortly after laying (Hauber and Sherman 2001; Moskát and Hauber 2007). The experimental separation of these 2 cognitive mechanisms, especially when both processes contribute to rejection behaviors, requires specially designed experimental treatments of one or most of the eggs in the nest to assess the relative contributions of these cognitive rules (Moskát et al. 2010).

In all cases of egg recognition, an internal rule based on memory or perceptual threshold could also guide discrimination decisions between acceptance and rejection, independent of the presence and diversity of the eggs that can be inspected and viewed in the nest at the time of the rejection decision (Lotem 1993; Hauber et al. 2006; Moskát and Hauber 2007). For example, variation in the difference of the perceived colors of foreign eggs from the memorized color template of own eggs may guide behavioral outcomes between acceptance and rejection (Reeve 1989; Hauber and Sherman 2001; Hauber et al. 2006; Igic et al. 2012).

Irrespective of the exact type and timing of recognition template acquisition, theory predicts that using multiple, nonexclusive cognitive processes of discrimination to generate a critical behavioral response may be especially beneficial in reducing recognition errors (i.e., mistakenly rejecting own eggs or accepting foreign eggs, through cognitive redundancy; e.g., Hauber et al. 2000). Integrating alternative decision rules to detect foreign eggs might be especially important in those host populations, where parasitic egg mimicry and parasitism rates are high and where clutches are often exposed to multiple parasitism (Moskát et al. 2009). In these cases, hosts' own eggs may be outnumbered by the several parasitic eggs or, in extreme cases, may be altogether replaced and absent from host nests during the laying or the incubation period (e.g., Rothstein 1974; Trine 2000; Hoover 2003; Gloag et al. 2012). Cuckoos parasitize great reed warblers in Hungary at unusually high rates, with more than 50% of nests parasitized in habitats, where trees are available as vantage points for cuckoos (Røskaft et al. 2002; Moskát et al. 2008b). A consequence of heavy cuckoo parasitism is the high frequency of multiple parasitism (Moskát et al. 2009). Previous work in Hungary also revealed that the presence of more cuckoo eggs, and therefore, reduced numbers of host eggs in a clutch are predictive of reduced rates of foreign egg rejection, including natural and experimental clutches with multiple parasitism (Moskát and Hauber 2007; Moskát et al. 2008a; Moskát et al. 2009). Critically, however, in all these prior studies, naturally or experimentally parasitized clutches included 1 or more host eggs, leaving possible the in situ simultaneous, online viewing and inspecting of own and foreign eggs in the nests, and thus, allowing for both discordancy and online self-referencing-based recognition mechanisms (sensu: Hauber and Sherman 2001).

Here, we manipulated the frequency and appearance of foreign eggs in host clutches to determine the relative contributions of each potential cognitive mechanism to egg rejection in great reed warblers. Specifically, our manipulations modified the relative applicability of both discordancy- and self-referencing-based cognitive rules, to assess their relative contributions to egg rejection decisions. We hypothesized that in single parasitism, hosts use several mechanisms for egg recognition, including discordancy, online self-referencing, and/or template recognition, but in multiple parasitism, template recognition plays a greater role, especially in the case where only parasitic eggs are in the clutch. Because the redundancy of different cognitive mechanisms is predicted to increase the accuracy of rejections (Reeve 1989), we predicted higher rejection rates of foreign eggs in single than in multiple parasitism. We tested the alternative hypothesis that the presence of own eggs in a mixed clutch of own and parasitic eggs increased hosts' egg recognition rates through online self-referencing. This hypothesis predicted that great reed warblers reject more foreign eggs in multiple parasitism, when hosts' own eggs are still present (albeit in the minority), relative to clutches where all of the hosts' own eggs are experimentally replaced with foreign eggs. However, the 2 different cognitive mechanisms are predicted to result in the identification of different "foreign" eggs in clutches, where the hosts' own eggs are outnumbered (self-referencing: foreign eggs; discordancy: own eggs). Regarding the experimental treatment when all hosts eggs are manipulated, we predicted that the third cognitive mechanism, an internal recognition template-based rejection decision (Moskát and Hauber 2007), must be operating. The use of varying numbers of dyed foreign eggs thus allows us to specifically test this third, recognition template mechanism, which predicts a consistent pattern of relative rejection rates of the same colored eggs across each of our treatment types.

To evaluate these hypotheses, we used a range of artificial colors to dye hosts' own eggs in order to determine whether color-dependent egg rejection rates in great reed warblers are elicited according to the presence and proportion of own eggs in the clutch. Additionally,

when the variation of parasitic egg appearances was reduced, that is, all eggs were dyed with 1 single color, we hypothesized that neither discordancy nor online self-referencing could yield egg discrimination. Therefore, if hosts used template-based egg discrimination, we predicted similar egg rejection rates to those in the treatment with all eggs dyed multiple colors. Alternatively, we predicted lower rejection rates in the multiple color treatments than in single parasitism's with the respective colors if the processes of discordancy or self-referencing were still required to correctly identify foreign eggs.

MATERIALS AND METHODS

The study was conducted in the surroundings of Apaj (47°07'N; 19°06'E), ca. 40–60 km south of Budapest, Hungary, in 2009, 2010, and 2012, from mid-May until mid-June. Great reed warblers breed in 2–4-m wide reed-belts along both sides of irrigation channels. We monitored sections of the channels weekly, in order to find nests during the nest-building or egg-laying stages. On the day of laying the 5th egg in the clutch (the modal clutch size in this host population: Moskát and Hauber 2007), 1 or more host eggs in a clutch were experimentally manipulated using highlighter pens (Stabilo Boss™). We applied blue, green, yellow, orange, and red highlighter pens (No. 70/31, 70/33, 70/24, 70/54, and 70/40, respectively) for dyeing the hosts' eggs. We used an Ocean Optics USB 2000 spectrometer to take representative reflectance spectra of the differently dyed host eggs, illustrated in Figure 1. Dyeing the hosts' own eggs is appropriate for experimental parasitism of great reed warblers because the parasite and host eggs are comparable in size (Honza et al. 2001; Török et al. 2004; Antonov et al. 2006). Although cuckoo eggs are thicker and stronger than host eggs (Hargitai et al. 2010; Igic et al. 2011), this relatively large host species is able to reject natural, stronger cuckoo eggs by puncture

ejection, and presumably, utilize the same rejection mechanism successfully for dyed own eggs (Honza and Moskát 2008). Accordingly, highlighter-dyed host eggs were found to be ejected consistently by this host species in several previous studies (Avilés et al. 2009; Moskát et al. 2009, 2010). Although these colors differ extensively from those of natural host or cuckoo eggs, they are still well within the avian visible light spectrum of 400–700 nm (Figure 1). Both prior work and this study (see below) yielded rejection rates of such artificially colored eggs by this host species that encompassed the range of egg rejections of natural cuckoo eggs (~40% and 12% rejection rates in single and multiple parasitism, respectively; Moskát et al. 2009).

We controlled for the experimental treatment within clutches by handling and inspecting all unmanipulated eggs to the same extent as dyed eggs. Prior experiments using dyeing treatments that left host egg background colors visible showed no significant differences in rejection rates between manipulated and unmanipulated eggs (Hauber et al. 2006), implying that dyeing host eggs does not elicit rejection behavior of undyed own eggs in this host species. Here, too, no unmanipulated eggs in the control nests (no dyeing treatment) were ejected or abandoned in this study ($n = 27$ nests).

One of the following 4 treatments was applied to each nest (Figure 2):

(a) Treatment "1 egg": We manipulated 1 host egg per clutch (single parasitism, where the foreign egg is in minority), using application of 1 of 5 color types at a time, with 1 of the 5 highlighter pen colors at a clutch, so the original maculation pattern also remained visible. We manipulated nests in the second-half of the laying stage, when 3–5 eggs were already in the nest, as earlier studies on this population revealed no difference between host responses to parasitism across the laying stages of having 2–5 eggs (with modal clutch size of 5 eggs) (e.g., Moskát and Hauber 2007).
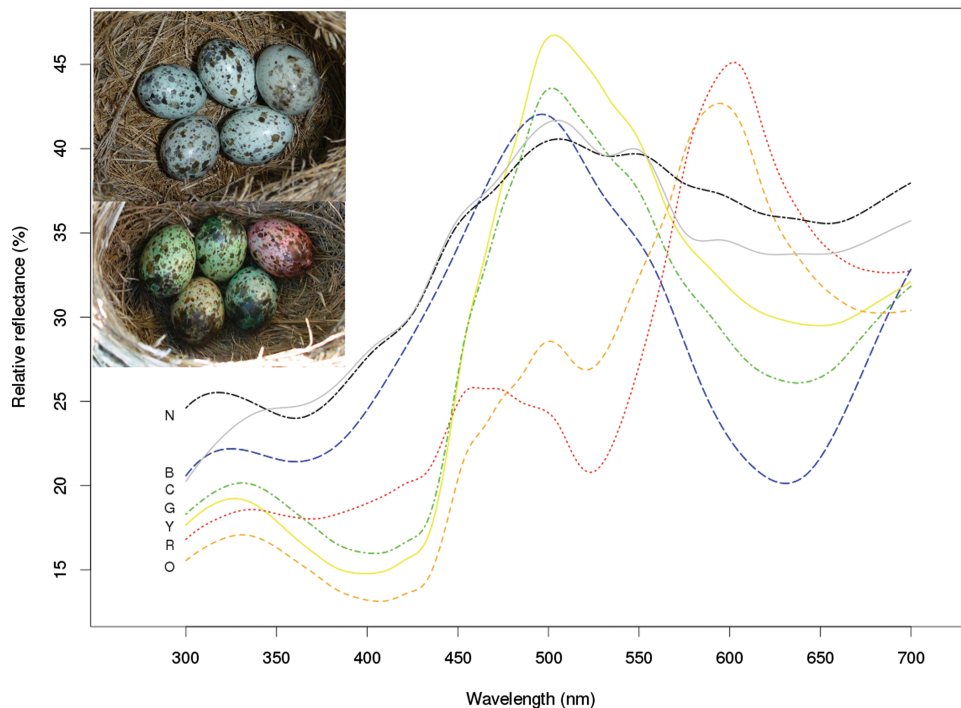

Figure 1
Photographic exemplars of a natural great reed warbler clutch parasitized by 1 cuckoo egg (on the right side of the nest), an experimental nest with 5 differently dyed host eggs, and the mean reflectances, relative to white standard (following the methods spectrometric data collection of Moskát et al. 2012), of the background of natural great reed warbler eggs (N), natural cuckoo eggs (C), and experimental eggs dyed with 1 of 5 different colors (blue: B; green: G; yellow: Y; red: R; or orange: O). Photo: István Zsoldos and Csaba Moskát.
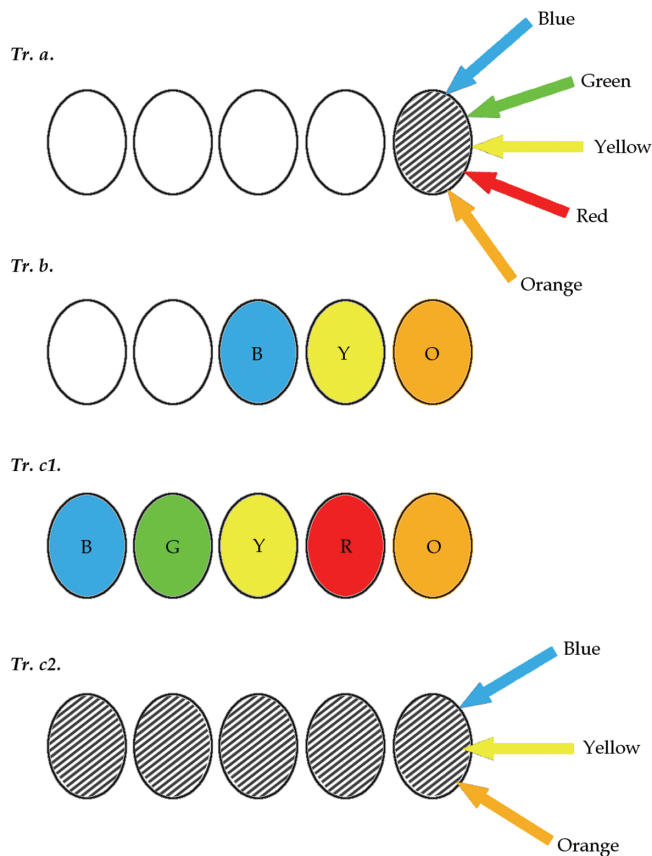
Figure 2

The experimental schematics of the treatment (Tr.) types for testing egg ejection in single (*a*) and multiple parasitism, either when 2 natural colored own eggs (white) of the host are present (*b*) or when none are present in the clutch (*c1*: 5 eggs dyed with different colors; *c2*: 5 eggs dyed with the same color). Five colors were applied for treatments (*a*) and (*c1*): blue, green, yellow, red, and orange, and 3 colors were used for treatments (*b*) and (*c2*): blue, yellow, and orange.

(*b*) Treatment "3 eggs": We manipulated 3 eggs (multiple parasitism, where the foreign eggs are in majority) in a clutch with different colors, using the blue, yellow, and orange pens. These colors alone evoked low, intermediate, and high rejection frequencies in our single parasitism treatments (our unpublished results). All experiments were started when clutches were completed with 5 eggs.

(*c1*) Treatment "5 eggs with multiple colors": All eggs in 5-egg clutches (multiple parasitism without unmanipulated eggs) were dyed, each with a different color from the same 5 colors as used in treatment (*a*). Experiments were started when clutches were completed with 5 eggs.

(*c2*) Treatment "5 eggs with 1 color": All eggs in 5-egg clutches (multiple parasitism without unmanipulated eggs) were dyed with 1 of the same 3 colors as used in treatment (*b*).

Experimental nests were monitored daily for 6 days after treatment in order to characterize host response to parasitism (Grim et al. 2011). If the manipulated eggs remained in the clutch at the end of the monitoring period (6 days), the egg(s) were considered accepted (following: Moksnes et al. 1991; Hauber et al. 2006; Moskát et al. 2010). To determine if a clutch was deserted, we looked for cold eggs and the lack of rotation of the eggs between daily visits. To look for egg rotation by females specifically, we positioned the eggs with their sharp poles toward the center of the

nest. If this configuration was not altered within 1 day and the eggs also remained cold, we categorized the result of the experiment as desertion. If the host removed 1 or more eggs from clutch, the result was classified as ejection.

We did not color band individual hosts in this study, but avoided pseudoreplication by including only nests that were sufficiently distant and synchronous within years to belong to different pairs. Pseudoreplication is also unlikely between years because this host species shows a low level of breeding philopatry in our study population (Moskát et al. 2008b). Accordingly, we considered each nest as the unit of statistical analysis.

Only nests which were not naturally parasitized by cuckoos were used for analyses to avoid the effect of external cues of parasitism (Svennungsen and Holen 2010), such as sight of the adult cuckoo (Davies and Brooke 1988) and the differential confounds of sequential (Hauber et al. 2006) versus simultaneous multiple parasitism (Moskát et al. 2009). We modeled parasitic egg ejection across treatments using linear models. The 2 cases of desertion in categories *a* and *c1*, both in response to green color, were excluded from the analyses.

We compared the outcomes across our treatments using a generalized linear mixed effects model (Bates and Maechler 2009) with logit link function and binomial error distribution. Here, the response variable was the ejection event of single eggs (binary factor), with laying date as a covariate and type of treatment as a fixed factor. Clutch ID was entered as random effect. With this model, we could also estimate the interaction between individual colors and treatments on egg ejection rates, allowing us to assess whether individual colors have their own differential effects versus the number(s) of painted eggs. In this model, we only considered the rejection rates of blue, yellow, and orange dyed eggs, which were present in all treatment types. The model was fitted using the Laplace approximation criterion (Bates and Maechler 2009). We used nonparametric rank tests to determine the relative rejection rates of differently dyed eggs across all treatments and to look for a statistical interaction effect between the number of eggs manipulated (*a*: 1, *b*: 3, or *c1* and *c2*: 5) and the number of colors used for manipulations per nest (*a*: 1, *b*: 3, *c1*: 5, or *c2*: 1). We used 2-tailed tests and set α = 0.05. For the analyses, we used the R statistical environment (R Development Core Team 2009) and Statview 5.0.1 (SAS, Cary, NC).

RESULTS

Altogether, 134 nest treatments produced usable outcomes (i.e., were not depredated, parasitized naturally by common cuckoos, or destroyed by storms before response could be recorded at 6 days following a manipulation). As we did not use nest desertion without ejection in our rejection calculations (1 case of desertion was detected in treatment *a* and 1 case in treatment *c1*, see above), our data set included 69 cases of single parasitism (treatment *a*; blue: $n = 14$, green: $n = 14$, yellow: $n = 12$, red: $n = 16$, and orange: $n = 13$), 16 cases for multiple parasitism with 3 manipulated eggs per clutch (treatment *b*), 16 cases for multiple parasitism with 5 differently manipulated eggs per clutch (treatment *c1*), and 33 cases in the 3 color categories for the multiple parasitism with 5 identically dyed eggs (treatment *c2*). The manipulation of egg coloration induced a broad range of reaction from hosts; ejection rates of these egg types varied widely (7–77%) in treatment (*a*) (Figure 3).

We observed 1 recognition error (i.e., the ejection of own egg(s); Davies and Brooke 1988; Stokke et al. 2002) without the ejection of the parasitic egg in treatment (*b*), where 1 host egg was ejected. Ejection cost (i.e., ejection of own egg together with 1 or more host
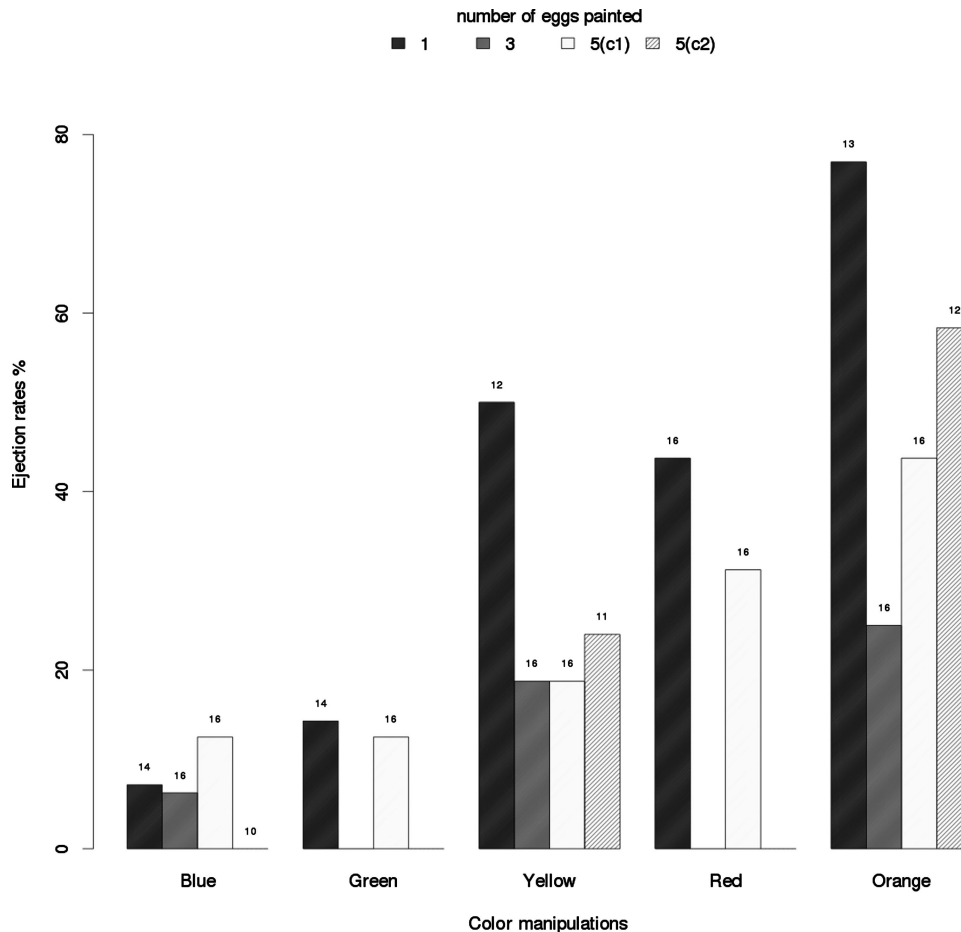
Figure 3

The proportion of nests where at least 1 manipulated egg was ejected by hosts in response to experimental parasitism with dyed own eggs. Note that number of colors was 5 in treatments *a* and *c1*, whereas the number of colors was 3 in treatments *b* and *c2*, and did not include green and red, and only 1 color per nest was used to dye host eggs in treatments *a* and *c2*. The details of each treatment are specified in Figure 2.

egg(s); Davies and Brooke 1988; Stokke et al. 2002) was also rare. Three such nests were found in treatment *a*: 2 nests where 1 or 4 own eggs were ejected when the experimental egg was dyed yellow, and 2 own eggs were ejected when the experimental egg was dyed red. Only 1 host egg was rejected in treatment *b*, where hosts also ejected 1 yellow egg and 1 orange egg from the 3 dyed eggs. In a few cases, hosts abandoned their nests after successful ejection of 1 or more parasitic eggs; such desertions occurred in treatment *c1* in 3 nests, where 1, 3, or 4 eggs were ejected per clutch prior. These postejection nest desertions in great reed warblers are regarded as the consequence of reduced clutch size (Moskát et al. 2011). Latency (in days) of egg ejection across treatments was greatest in treatment *a*, intermediate in treatment *b*, and the smallest in treatment *c2* (mean ± standard error [SE]: *a*: 2.31 ± 0.26, *n* = 26; *b*: 1.89 ± 0.42, *n* = 9; *c1*: 1.58 ± 0.23, *n* = 19; *c2*: 1.27 ± 1.95; *n* = 11; Kruskal–Wallis test, χ^2 = 7.84, df = 3, *P* = 0.049).

Laying date had no significant effect on egg ejection (*B* = -0.237, SE = 0.14, *z* = -1.693, *P* = 0.09; Table 1), whereas the color of the dyed egg significantly affected host responses (blue: *B* = -4.864, SE = 1.917, *z* = -2.536, *P* = 0.011; yellow: *B* = 3.801, SE = 1.457, *z* = 2.608, *P* = 0.009; orange: *B* = 7.053, SE = 1.763, *z* = 4.0, *P* < 0.001; Table 1). Ejection rates increased in the following order: blue < green < red/yellow < orange across the treatments (Figure 3).

To investigate the effect of number of eggs painted on ejection rate across the 3 treatments, we compared ejection rates of eggs

Table 1

Estimates of ejection rates ($\log_{10}$ transformed values) for experimental egg colors and treatments. Generalized linear mixed models were fit by the Laplace approximation, with reference category of "ejection of single blue eggs"

Ejections	B	SE	z	P
Intercept	-4.86	1.92	-2.54	0.01
Laying date	-0.24	0.14	-1.69	0.09
Yellow	3.80	1.46	2.61	0.01
Orange	7.05	1.76	4.00	<0.01
Treatment (*b*)				
Painted 3 eggs	-7.57	3.15	-2.40	0.02
Treatment (*c1*)				
Painted 5 eggs	-4.91	2.54	-1.93	0.05
Treatment (*c2*)				
Painted 5 eggs	-3.26	2.31	-1.41	0.16

dyed blue, red, or orange, as these 3 colors were present in all treatment groups and hence allowed the calculation of interaction between egg color and number of eggs painted. Ejection rate was significantly lower for eggs in clutches containing 3 colored eggs (treatment *b*) than for eggs in clutches with 1 (treatment *a*) painted egg (*B* = -7.571, SE = 3.151, *z* = -2.403, *P* = 0.016; Table 1). Host responses across the 3 treatments involving multiple parasitism (treatments *b*, *c1*, and *c2*) were statistically similar when ejections

per nest were considered binary (yes/no) ($B = 1.264$, SE $= 1.069$, $z = 1.183$, $P = 0.237$).

The interaction between egg color and the number of eggs painted was not significant ($P > 0.39$), therefore, we removed the interaction term from the final model. This lack of significant interaction showed that the rank order of ejection rates of egg colors used in all 3 treatments (blue, yellow, and orange; treatments *a*, *b*, *c1*, and *c2*) was consistent across treatments. Accordingly, the relative rank of ejection rates of those 3 egg colors was significant across the 3 treatments, with relative ejection rates of blue < yellow < orange egg colors (nonparametric Friedman Anova: $\chi^2 = 8.00$, $P = 0.018$). This implies that the number of total egg colors in the manipulation did not significantly impact the relative patterns of color-based egg ejection decisions of these cuckoo hosts.

DISCUSSION

We demonstrated that there are consistent patterns of egg rejection in response to experimental avian brood parasitism in the presence or absence of hosts' own eggs such that host egg presence is not necessary for foreign egg recognition. Across our treatments, we obtained the strongest rejection responses to experimentally dyed eggs when host nests contained 1 (treatment *a*) as opposed to 3 or 5 experimentally dyed "parasitic" eggs (treatments *b*, *c1*, and *c2*, respectively). Even though these manipulations included different combinations of colors and varying numbers of dyed eggs, we detected no interaction between the number of eggs and colors experimentally introduced in generating responses to parasitism, so the results support our prediction that hosts' egg rejection responses are reduced in multiple parasitism (Moskát et al. 2009) irrespective of parasitic egg color variation. Critically, in the treatments where all eggs within a clutch were dyed (treatments *c1* and *c2*), hosts could no longer use online comparison of own versus foreign eggs, through either self-referencing own eggs or discordancy between own and foreign eggs. Despite this, hosts continued to consistently reject foreign eggs based on their coloration with the same relative probability as in nests with some or the majority of their own eggs visible. We suggest that in this context, hosts can use an internal template recognition rule, assessing whether the potential parasitic egg's appearance falls within the acceptance threshold based on the appearance of the internal template (Reeve 1989; Servedio and Lande 2003) to decide whether or not to eject a given egg (Hauber et al. 2006; Moskát and Hauber 2007).

Hosts did not reject all dyed or foreign eggs in treatment *b*, in which both self-referencing and filter-based recognition mechanisms were available to identify foreign eggs. In the case of orange eggs, they did so statistically less often than when no own eggs were visible in the nest (treatment *c1*). One explanation is that in the case of 3 parasitic eggs and 2 own eggs (treatment *b*), hosts employ a special discordancy-based mechanism along with the recognition template-based discrimination mechanism. This effect would then predict lower overall rejection rates in multiple parasitism with several foreign and own eggs present in the nest; this reduced-accuracy discordancy would also explain our previous results, when we revealed a higher tolerance for variably mimetic cuckoo or manipulated eggs in multiple than in single cuckoo parasitism (Moskát et al. 2009).

In one of our earlier studies (Moskát et al. 2010), we documented that great reed warblers ejected 1 own egg from 10% of clutches ($n = 30$ clutches) containing 4 experimentally manipulated ("parasitic") eggs and 1 own natural egg per clutch. In this study, we found only 1 case where 1 host egg was ejected in treatment

b ($n = 16$ clutches in this category). In this treatment, 3 differently manipulated ("parasitic") eggs and 2 own eggs were present in the nest. Although our sample size is not suitable for a detailed comparison of host reactions to their own eggs in different types of multiple parasitism events, we expect some ejections of these eggs if discordancy, rather than template recognition alone, also affects egg recognition (Moskát and Hauber 2007; Moskát et al. 2010). Great reed warblers reject fewer parasitic eggs (both natural and artificial parasitic eggs) from multiple- than single-parasitized clutches (Moskát et al. 2009). Consequently, and in accordance with our present and previous results (see Moskát et al. 2010), discordancy should be less accurate in detecting foreign eggs when more than 1 egg of the minority egg type is presented, than in cases when only egg per clutch is of the minority egg type.

In contrast to our described host species, the brambling *(Fringilla montifringilla)* and chaffinch *(Fringilla coelebs)* express similar rejection rates in single and multiple parasitism with 2 parasitic eggs (Vikan et al. 2009). Therefore, these finch species are likely to detect parasitic eggs by recognition template only, and not to rely on discordancy-based discrimination, as do great reed warblers (Moskát et al. 2010). In contrast to the ongoing arms race between cuckoos and great reed warblers, those 2 finch species have been nearly fully abandoned as hosts by the cuckoo throughout Europe (Vikan et al. 2009, 2011; Avilés et al. 2010), implying a nearly terminated coevolutionary history with this brood parasite. In support of these different evolutionary histories, theoretical models predict that those host species, which tolerate more cuckoo eggs in multiple than in single parasitism, would have been exposed to longer coevolutionary interactions. The great reed warbler is a good example for this phenomenon, which shows stable host–brood parasite population dynamics (Takasu and Moskát 2011).

A critical treatment in our experiment included an all-clutch manipulation, where each of the hosts' 5 eggs was dyed with either different or same colors. The results of the absolute rejection rates showed consistent decreases from single-egg to the multiple-egg treatments. In contrast, the relative rejection rates of eggs of specific colors remained consistent between the single-egg and the 5-egg experiments in that blue eggs were accepted the most and orange eggs were accepted the least often. We conclude that these hosts possess a consistent relative color-based sensory acceptance threshold for foreign egg colors, but whether those foreign eggs elicit responses and are rejected may be modified by context, including the proportion of hosts' own eggs present in the nest. An additional critical interpretation of these data is that hosts recognize more eggs than they actually reject (Lyon 2003; Moskát and Hauber 2007). This conclusion also has implications for the cognitive decision rules involved in mediating behavioral responses through sensation and perception. Specifically, the new results reveal that the lack of behavioral responses to foreign eggs is not necessarily due to limited cognitive complexity of host birds (Moskát and Hauber 2007; Antonov et al. 2009; Soler et al. 2012), as the color effect on egg ejection was more important than the effect of the number of parasitic eggs.

Overall, great reed warblers' rejection rates of dyed eggs depend on the number and type of experimental eggs per clutch, from the highest rates in treatment *a* to lower rates in treatments *b*, *c1*, and *c2*. In turn, the relative proportions of differently dyed eggs rejected in each treatment showed a consistent pattern across all 3 treatments, with blue eggs most likely to be accepted and orange eggs most likely to be rejected. Given that both the presence/absence and also the relative numbers of great reed warblers' own eggs over dyed eggs varied globally across these experiments, these results are

most consistent with a recognition template-based discrimination mechanism operating in these hosts in response to sensory inputs from particular colors of foreign eggs. Because we manipulated host eggs at clutch completion, our results do not reveal whether hosts need to view their own eggs during the current or a past laying attempt to acquire their internal recognition template. Future experiments should address egg rejection behavior in young hosts, which have not had the chance to inspect their own eggs even once (Victoria 1972).

CONCLUSION

Recognizing and eliminating foreign eggs is an effective and early line of defense against virulent cuckoo brood parasitism (Kilner and Langmore 2011; Feeney et al. 2012), whose young remove all host eggs and nestlings from parasitized broods (Anderson et al. 2009; Grim 2006). However, no rejection mechanisms are fail-proof (Reeve 1989), and hosts of social parasites must employ cognitive processes, which not only increase the chance of detecting foreign young but also reduce the chance of mistakenly rejecting one's own young (Servedio and Lande 2003). Here, we demonstrate a cognitive duality in the egg rejection success of a cuckoo host by showing that (1) increasing the number of foreign egg types in the nest decreases the likelihood of correctly recognizing foreign eggs, and yet, even when all of own eggs are replaced by foreign eggs, (2) these hosts are still able to reject foreign eggs without having to simultaneously view their own and the foreign eggs. Using an approach of extensive, coherent, and consistent experimental treatments on host versus foreign eggshell background colors here, our results parallel prior experimentation and outcomes relevant to the role of eggshell maculation (Moskát et al. 2010). Taken together, these patterns support the general hypothesis that through cognitive alternatives, decision-making processes generate a type of redundancy, which in turn functions to increase the context-dependent accuracy of evolutionarily critical recognition decisions between self and others (Hauber et al. 2000; Campobello and Sealy 2011).

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