BRILL Behaviour (2012) DOI:10.1163/156853912X638445

Behaviour
brill.nl/beh

Asymmetrical signal content of egg shape as predictor of egg rejection by great reed warblers, hosts of the common cuckoo

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Accepted 20 March 2012

Abstract

The size, patterning and coloration of bird eggs may signal different information content to nest owners, mates, predators, hosts, or brood parasites. Recent studies suggested that the pigmentation at one pole of the typically asymmetrical avian egg plays a critical role in the discrimination of own and foreign eggs by several host species parasitized by the common cuckoo (*Cuculus canorus*). Typically, both eggshell maculation and background colour are more consistent on the blunt pole, and hosts react more strongly to experimental changes in coloration of the blunt pole compared to the sharp pole. However, it remains unclear whether the asymmetrical shape of natural eggs *per se* enhances the behavioural responses of hosts to foreign eggs. To evaluate the salience of asymmetrical egg shape, we studied reactions of a rejecter cuckoo host, the great reed warbler (*Acrocephalus arundinaceus*), to artificial shapes of model eggs painted a non-mimetic blue colour. Artificial eggs with two blunt poles were rejected significantly more often than those with a single blunt pole or two sharp poles. These results corroborate the hypothesis that the different egg poles have different signal salience and may have implications for the evolution of diversity of not only egg coloration but also of egg shape in the arms race between hosts and brood parasitic birds.

Keywords

egg shape, brood parasitism, recognition cues, signal salience.

DOI:10.1163/156853912X638445

1. Introduction

Signals are evolved display behaviours, sensory cues, or morphological structures that induce a specific response in the receiver (Maynard-Smith & Harper, 2003). Signals are used widely among animals in warfare, cooperation, and predator–prey interactions, and serve a central role in sexual selection through both intrasexual competition and intersexual choice for mates (Andersson, 1994; Hauber & Zuk, 2010). For example, coloration may serve several signalling roles through either similarity to the environment (e.g., crypsis, mimicry) or contrast against a backdrop (e.g., discordancy, unfamiliarity) (Hill & McGraw, 2006; Hubbard et al., 2010).

In birds, the diversity of eggshell coloration has been widely linked to subserve diverse functions, including camouflage and crypsis from predation and parasitism (Underwood & Sealy, 2002; Langmore et al., 2009), protection against breakage (Gosler et al., 2005), shielding from solar radiation (Lahti, 2008), preventing microbial infestation (Ishikawa et al., 2010), mimicry for brood parasitism (Moksnes & Røskaft, 1995; Kilner, 2006), signalling egg quality (Moreno et al., 2006; Hargitai et al., 2010) and eliciting parental care (Soler et al., 2005). There is particularly extensive comparative and experimental evidence that avian eggshell colours and maculation patterns play an important role in hosts' recognition of foreign eggs laid by brood parasites (Davies & Brooke, 1988; Røskaft & Moksnes, 1998; Honza et al., 2007; Cassey et al., 2008; Moskát et al., 2008; Stoddard & Stevens, 2010, 2011; Spottiswoode & Stevens, 2010). Sophisticated cognitive decision rules enabling egg discrimination have evolved in many hosts of an obligate brood parasite, the common cuckoo (*Cuculus canorus*) and of several other brood parasites, contributing to the recognition of own eggs and the rejection of foreign eggs (Hauber & Sherman, 2001; Moskát & Hauber, 2007; Moskát et al., 2010).

Recent egg discrimination studies on hosts of brood parasites have drawn attention to a previously unknown role of the characteristically asymmetrical shape of the avian eggshell, namely the coloration of its two different poles. Analysis of the colour and maculation of the eggs of potential common cuckoo hosts revealed that the blunt pole is more consistent in appearance in both the blackcap (*Sylvia atricapilla*) (Polaciková et al., 2007) and the song thrush (*Turdus philomelos*) (Polaciková et al., 2010, 2011). Experimental evidence also confirms that song thrushes, blackbirds (*T. merula*), great reed warblers (*Acrocephalus arundinaceus*) and reed warblers (*A. scirpaceus*) also react more strongly to manipulation of the coloration of the blunt pole (BP) than that of the sharp pole (SP) (Polaciková & Grim, 2010; Polaciková et al., 2010). These results call for more detailed analyses of the relative salience and the potential interaction of the contributions of egg shape and coloration in shaping cognitive decision rules in hosts of brood parasites to reject foreign eggs (Alvarez et al., 1976; Bán et al., 2011; Polaciková et al., 2011).

As a result of the coevolutionary arms race (Dawkins & Krebs, 1979) between the parasitic common cuckoo (hereafter: cuckoo) and one of its preferred hosts, the great reed warbler, this host species has evolved fine-tuned egg recognition abilities (e.g., Moskát & Hauber, 2007), as well as relatively extensive interclutch variation in egg coloration at the population level (Moskát & Honza, 2002; Cherry et al., 2007). Previous studies on this host-parasite system showed that hosts reject non-mimetic parasitic eggs at a high rate (Hauber et al., 2006), and patterning (i.e., maculation) is of secondary importance to background coloration in eliciting egg rejection (Moskát et al., 2008, 2010).

While the salience of eggshell colour and maculation in hosts' foreign egg recognition is intensively studied (see above), it is still unclear how the shape of the parasitic eggs may affect egg recognition. Critically, many hosts discriminate against generally non-egg-shaped objects (Rothstein, 1975; Ortega & Cruz, 1988; Hauber, 2003; Moskát et al., 2003; Underwood & Sealy, 2006a; Guigueno & Sealy, 2009), although this behaviour is also found in bird species that are non-hosts to brood parasites (Thomson, 1934; Tinbergen et al., 1962; Welty, 1982). Accordingly, several authors proposed that ejection of the parasitic eggs might have evolved from the general mechanism of nest sanitation, as birds eject twigs, leafs, pebbles, debris eggs, uneaten food, and dead chick (Rothstein, 1975; Kemal & Rothstein, 1988; Hauber, 2003; Moskát et al., 2003; Underwood & Sealy, 2006a; Guigueno & Sealy, 2012). Ejection of eggs that differ in shape from hosts' own eggs seems to be a reliable and efficient decision rule to identify parasitic eggs. Thus, a fine-tuned egg ejection ability of a host may increase egg ejection frequencies toward increasingly non-own-egg-shaped objects as a side-effect (Rothstein, 1975; Moskát et al., 2003; Guigueno & Sealy, 2012). Critically, for example, common cuckoo's eggs are similar in size but different in shape to great reed warbler's eggs (Bán et al., 2011). However, own-egg-shape recognition itself, in the absence of egg colour recognition, might generally exist in many host (and non-host) species, although studies that provide support for the relative role of this phenomenon in the detection and rejection of foreign eggs are scarce (Marchetti, 2000; Guigueno & Sealy, 2012).

We used model eggs of novel egg shapes, as well as naturally asymmetrical (control) shaped model eggs, placed into nests in a great reed warbler population that is heavily parasitized by cuckoos ($>50\%$ of nests: Moskát & Honza, 2002). We tested the reaction of hosts to artificial eggs, by focusing on the hypothesis that sensory cues from the blunt pole are required for egg recognition to be manifested through behavioural rejection responses. Accordingly, we predicted that artificial eggs with two blunt poles would be rejected more often than eggs with only sharp poles, and that artificial control shaped eggs having of both a blunt and a sharp pole would be rejected at intermediate rates. In contrast, the asymmetrical eggshell shape recognition hypothesis predicted that control artificial eggs would be rejected the least often, while experimental eggs with either two blunt poles or two sharp poles, would be rejected more often.

2. Methods

Fieldwork was carried out in the vicinity of Apaj (47°07′N; 19°06′E), ca. 50 km south of Budapest, Hungary, between mid-May and mid-June in 2010, the area of our long term research on common cuckoos and their hosts (for more details on the study site and study species, see Moskát & Honza, 2002). We systematically searched the 2–4 m wide reed beds of narrow irrigation channels for nests of the great reed warbler (GRW) twice a week, and found most nests in the building stage or during the laying stage. On the day when the clutch was predicted to have 5 host eggs (i.e., the typical clutch size for this host, with one egg laid per day), we exchanged one great reed warbler egg for one of our artificial eggs. Eventually, at 22 nests, the host's clutch size was 5 eggs, at 7 nests it was 4 eggs, and at 1 nest it was 6 eggs.

The following artificial egg types with novel shapes were used (Figure 1): (i) eggs with two blunt poles (2 × BP), and (ii) eggs with two sharp poles (2 × SP), as well as (iii) eggs with a blunt and a sharp pole (control egg) (Figure 1). All three types of artificial eggs were made out of thermoset plasticine ('Creal-therm Professional' Modelling Material, following the protocol of Bártol et al., 2002 and Antonov et al., 2009 with a polystyrene kernel, painted dark blue with acrylic paint (PANTONE code 300C). We used this colour

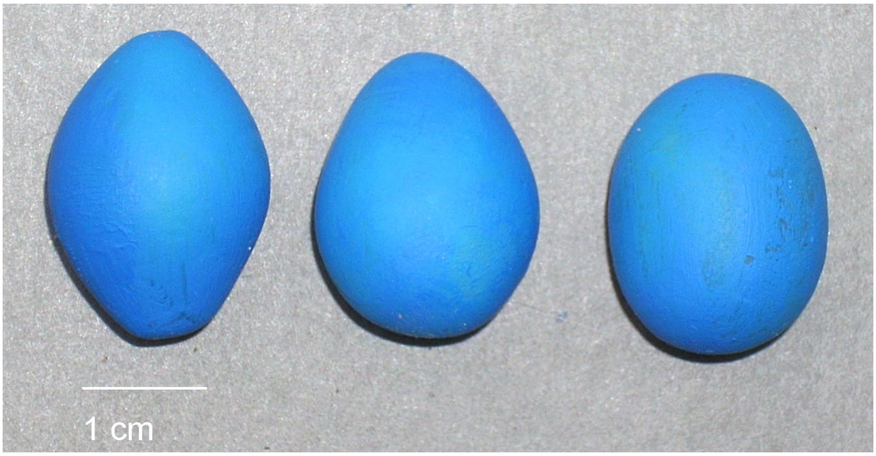

Figure 1. Three types of model eggs used for studying the role of egg shape in behavioural egg rejection experiments: a novel egg with two sharp poles (left: 2 × SP), a control shaped egg with one blunt and one sharp poles (middle), and a novel egg with two blunt poles (right: 2 × BP). This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/beh

to make our results comparable with the experimental study of Polaciková & Grim (2010), where the authors used the same colour when they dyed the blunt or the sharp pole of real GRW eggs in the Czech Republic (L. Polaciková, pers. commun.). These asymmetrically painted dark blue artificial eggs in prior experiments with GRW were reported to be rejected at intermediate rates (21–67%, Polaciková & Grim, 2010), so this colour was also predicted to elicit measurable variation in the rejection or acceptance responses by this host species (Samas et al., 2011). The three egg types were manufactured so that they were comparable to real GRW or cuckoo eggs both in size and weight, as the host and parasite eggs have overlapping volumes in our population (Hargitai et al., 2010). As the dimensions of the three model egg types were specifically standardised by weight (Table 1), consequently the 2 × BP eggs were somewhat shorter and wider than 2 × SP eggs, while model eggs with the control egg shape were intermediate (Kruskal–Wallis ANOVA: length: $F_{2,27} = 50.09$, $p < 0.001$, width: $F_{2,27} = 0.892$, $p = 0.422$, weight: $F_{2,27} = 0.174$, $p = 0.083$). However, small deviations in egg size were not a factor that influenced the frequency of egg rejection in most cuckoo-host systems in which the parasite evolved egg mimicry (Antonov et al., 2006; Stokke et al., 2010).

Table 1.
Size parameters of model eggs used for experimental parasitism (means ± SE).

	Length (mm)	Width (mm)	Weight (g)
2 × SP	24.0 ± 0.24	17.0 ± 0.26	3.4 ± 0.09
Control egg	22.2 ± 0.19	17.0 ± 0.12	3.4 ± 0.06
2 × BP	20.9 ± 0.23	17.3 ± 0.14	3.6 ± 0.09

2 × SP, model egg with two sharp poles; control egg, normal egg-type model egg with one sharp and one blunt poles; 2 × BP, model egg with two blunt poles.

Only GRW clutches that were not parasitized naturally by common cuckoos and not predated until the outcome of the experiments could be determined were used in the experiment. In previous works, the nests of the *Acrocephalus* warblers were monitored daily for 5–6 consecutive days or until the host rejected the artificial egg (e.g., Lotem et al., 1995; Moskát & Hauber, 2007; Pozgayová et al., 2009). We monitored experimental nests for 5 consecutive days in this standard manner: host reactions were categorised as acceptance, if the model egg remained in the nest at the end of the monitoring period; ejection, if the model egg was missing from the clutch, but the remaining eggs were found incubated; or desertion, if the nest was not active, indicated by cold eggs and no rotation of eggs (i.e., incubating GRW frequently move and rotate their eggs, and so we considered a nest deserted if cold eggs, after arranging them with their sharp poles pointing to the centre of the nest, remained in the same position between nest checks during the next two daily visits).

2.1. Statistical analyses

We carried out a binary logistic regression analysis for the comparison of hosts' behavioural responses to dark blue 2 × SP, control and 2 × BP eggs. The full model included the host's response to parasitism as a binary dependent variable (accepted or rejected), treatment as a fixed factor, and laying date and clutch size as covariates. Laying date was considered a continuous variable from the laying of the first egg in any of our experimental nests in this year (May 19). We also tested for any interactions of the main predictors. Although hosts were not colour-banded, our study area was large (ca. 20 × 30 km), we avoided using other nests in the close vicinity of an already experimental nest (i.e., potential replacement clutches or the second broods of a pair in the same territory) and, thus, reduced the chance for pseudoreplication. For binary logistic regression we used nominal regression module in SPSS ver. 17.0 (SPSS, Chicago, IL, USA).

3. Results

Great reed warblers showed a wide range of responses to experimental parasitism with the three types of model eggs. Hosts rejected 50% of the 2 × SP eggs, 70% of the control eggs, and 100% of the 2 × BP eggs (Figure 2). Hosts rejected all types of eggs by ejection, except in one case in the 2 × BP treatment, where the nest was deserted. Great reed warblers rejected all types of our eggs quickly, most of them within 1 day (mean ± SE: 2 × SP 1.00 ± 0.00; control 1.57 ± 0.30; 2 × BP 1.10 ± 0.10). These values of latencies until rejection between the several parasitism treatments proved to be statistically similar (Kruskal–Wallis test, $\chi^2 = 2.830$, df $= 2$, $p = 0.112$). In post-hoc comparisons, host responses toward the two experimental egg types (2 × SP or 2 × BP) showed a significant difference between each other (Fisher's exact test, two-tailed, $p = 0.003$).

In the binary logistic regression, there was a significant overall effect on host responses ($B = 21.055$, SE $= 1.248$, Wald $= 284, 657$, df $= 1$, $p < 0.001$) for the three parasitism treatments with 2 × SP, control, or 2 × BP eggs. Neither laying date nor clutch size had significant effects

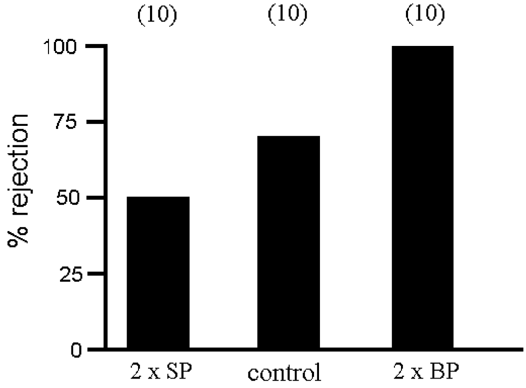

Figure 2. Great reed warblers' responses to experimental parasitism with three types of model eggs; from left to right: artificial-shaped egg with two sharp poles (2 × SP), painted immaculate dark blue; control egg with one blunt and one sharp poles, painted immaculate dark blue (control); and artificial egg with two blunt poles (2 × BP). Sample sizes are shown above bars.

($B = 0.213$, SE $= 0.142$, Wald $= 2.238$, df $= 1$, $p = 0.135$, and $B = 1.356$, SE $= 1.162$, Wald $= 1.363$, df $= 1$, $p = 0.243$, respectively).

4. Discussion

Our results support the hypothesis that the salience of different eggshell poles varies in eliciting behavioural decisions by hosts of avian brood parasites to reject foreign eggs. In our experiments, only half of the model eggs were rejected when these had two sharp poles, while all model eggs with two blunt poles were rejected. The rejection rate of the natural (asymmetrically shaped) control model eggs fell between those of the two artificial egg shapes. These results of the intermediate rejection rates of control model eggs also rule out the hypothesis that eggshell shape asymmetry per se contributes to the discrimination and rejection of foreign eggs because symmetrical eggs were rejected at both lower and higher rates compared to parasitism with the asymmetrical eggs.

Our results indicate that egg shape itself influences the rejection rate of foreign eggs, with rounder, symmetrical shaped eggs being rejected more often as compared to more elongated model eggs (Figure 2). In the absence of video-taping, and mechanical analyses of the beak and grasp mechanics (Antonov et al., 2008; Rasmussen et al., 2010), we do not know the proximate reasons for the variation in egg rejection rates due to eggshell shape itself in nests of great reed warblers. Nonetheless, we note that common cuckoo eggs have distinct, rounder shapes compared to great reed warbler eggs (Bán et al., 2011).

Our findings on the relevance of egg shape in egg discrimination extend the conclusions of Polaciková et al. (2007, 2010, 2011) and Polaciková & Grim (2010), whose studies revealed that coloration of the blunt poles of bird eggs played a more important role in behavioural measures of egg recognition responses than coloration at the sharp pole. Natural-shaped great reed warbler eggs are typically maculated, and have more spots at the blunt pole than at the sharp pole (Moskát et al., 2002; Polaciková & Grim, 2010; Polaciková et al., 2011), and such higher density and/or intensity of potential recognition cues may in turn contribute to better chances and greater accuracy of correct egg discrimination (Cherry & Gosler, 2010). Moreover, the overall surface area of eggshell around the blunt pole is evidently larger than around the sharp pole, so blunt poles have the potential for greater amount of information content of eggshell signals (Tufte, 1990). However, further research is needed to clarify how hosts use the information content of the eggshell at around the blunt pole, either the presence or the absence of special key characters of shape, colour, spottiness, and their potential interactions as compound signals.

There are several studies on the types and ranges of phenotypic cues that may serve as key factors in foreign egg recognition in common cuckoo hosts, and most often these involve coloration and maculation of the eggshell (e.g., Davies & Brooke, 1988; Røskaft & Moksnes, 1998; Cherry et al., 2007; Honza et al., 2007; Moskát et al., 2008; Cassey et al., 2008; Antonov et al., 2010; Avilés et al., 2010; Igic et al., 2012), and also in hosts of other obligate brood parasitic birds (Rothstein, 1982; Lahti & Lahti, 2002; Underwood & Sealy, 2006b), or species with exposure to conspecific brood parasitism (López-de-Hierro & Moreno-Rueda, 2010; Riehl, 2010). However, egg size (Rothstein, 1975, 1982; Marchetti, 2000; Underwood & Sealy, 2006b; Guigueno & Sealy, 2012) and egg shape (Underwood & Sealy, 2006a; Guigueno & Sealy, 2012) may also play a role in egg recognition per se, or contribute coloration- and maculation-based recognition rules in several hosts of different brood parasitic lineages. Egg-shape discrimination has been tested in hosts of brood parasites using various non-egg-shaped objects (e.g., Ortega & Cruz, 1988; Moskát et al., 2003), as well as over a range of different sized objects (Guigueno & Sealy, 2009, 2012). Magpies (*Pica pica*), hosts of great spotted cuckoos (*Clamator glandarius*), showed the quickest responses to egg shapes different from oval (i.e., spherical and cubical) than other stimuli, including egg colour, size, and weight (Alvarez et al., 1976). A more specific study in hosts of the brown-headed cowbird (*Molothrus ater*) revealed that rounded and spherical artificial eggs were rejected at similar levels as control parasitic eggs, but at lower levels relative to more odd-shape objects. Egg shape recognition is predicted to be most advanced in birds which can differentiate between non-egg items in the nest (e.g., owing to the benefits of nest sanitation of objects very dissimilar from eggs in shape), parasite eggs, and own eggs (cf., Peer et al., 2007; Guigueno & Sealy, 2009). In addition (but not mutually exclusively), egg shape discrimination between own and foreign eggs (as is possible in GRW: Bán et al., 2011), is also predicted in species where perceptual constraints on egg colour and maculation discrimination prevent the discrimination of own and highly colour-mimetic parasitic eggs, as also seen in GRW (Igic et al., 2012).

Our experiments here reveal that egg shape overall, and the presence of the blunt egg pole in particular, are both critical predictors of variation in egg rejection decisions in GRWs, even when non-mimetic coloration is already present as a cue for egg discrimination. In cuckoos, the longer evolutionary history together with their hosts in respect to cowbirds (Rothstein & Robinson, 1998; Davies, 2000) may cause the evolved accurate egg recognition ability, including the rejection of more rounded egg shape, as it was observed in our study.

Although some of the basic cognitive mechanisms of egg recognition rules and rejection behaviours have already been modelled (Davies et al., 1996; Rodríguez-Gironés & Lotem, 1999; Stokke et al., 2007; Svennungsen & Holen, 2010), these models typically include linear measures and combinations of host-parasite egg dissimilarity (e.g., Servedio & Lande, 2003; Servedio & Hauber, 2006), whereas many morphological triggers, including the possibility of non-linear trait combinations, such as those involved in shape (Bán et al., 2011), regarding the proximate cues salient for egg discrimination decisions, remain unknown. For example, different features of eggs may contribute synergistically or complementarily to evoke discrimination decisions (e.g., coloration and size, in American robins *Turdus migratorius*, rejecting brown-headed cowbird eggs: Rothstein, 1982). Similarly, egg shape and coloration may provide complementary cues to guide the rejection responses of hosts. Conversely, a different set of constraints may act on egg coloration, size, shape, or thickness, influencing the evolution of (im)perfect mimicry of host eggs by brood parasites (Johnstone, 2002; Avilés & Møller, 2004; Hauber et al., 2006; Takasu et al., 2009; Antonov et al., 2010; Spottiswoode & Stevens, 2010). For example, shell coloration and shape are each the result of several processes during egg formation and can contribute to different functions (Igic et al., 2011, 2012). Accordingly, shape is an important factor for both hatchability (Barta & Székely, 1997; Mao et al., 2007) and structural strength, including rounder parasitic cuckoo eggs (Honza et al., 2001; Hargitai et al., 2010; Igic et al., 2011). Here, we demonstrated that a particular pole of the asymmetrical avian egg shape, represents a potentially more salient recognition cue for host-parasite egg discrimination than other elements of the egg shape. It remains to be tested, however, whether the continued presence of a blunt pole in most avian eggs is a physiological or structural constraint related to the formation, laying, incubation, and hatchability of bird eggs, which cannot be easily overcome by brood parasites. Theoretically, it would seem to be an advantage for cuckoos to lay eggs with two sharp poles, as these would be experiencing a lower rejection rate than asymmetrical or round eggs.

Acknowledgements

The Middle Danube-Valley Inspectorate for Environmental Protection, Nature Conservation and Water Management, Hungary, kindly provided permissions for the research. The authors thank Miklós Bán, István Zsoldos and Tamás Lőrincz for help in the field. We thank Lenka Polaciková for advice. Funding for this research was provided in part by the Human Frontier in Science Program and PSC-CUNY (to M.E.H.), and also by the Hungarian National Science Fund (OTKA, No. 83217 to C.M.).

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