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Discordancy or template-based recognition? Dissecting the cognitive basis of the rejection of foreign eggs in hosts of avian brood parasites

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SUMMARY

Many avian hosts have evolved antiparasite defence mechanisms, including egg rejection, to reduce the costs of brood parasitism. The two main alternative cognitive mechanisms of egg discrimination are thought to be based on the perceived discordancy of eggs in a clutch or the use of recognition templates by hosts. Our experiments reveal that the great reed warbler (*Acrocephalus arundinaceus*), a host of the common cuckoo (*Cuculus canorus*), relies on both mechanisms. In support of the discordancy mechanism, hosts rejected their own eggs (13%) and manipulated ('parasitic') eggs (27%) above control levels in experiments when manipulated eggs were in the majority but when clutches also included a minority of own eggs. Hosts that had the chance to observe the manipulated eggs daily just after laying did not show stronger rejection of manipulated eggs than when the eggs were manipulated at clutch completion. When clutches contained only manipulated eggs, in 33% of the nests hosts showed rejection, also supporting a mechanism of template-based egg discrimination. Rejection using a recognition template might be more advantageous because discordancy-based egg discrimination is increasingly error prone with higher rates of multiple parasitism.

Key words: brood parasitism, egg discrimination, learning, discordancy, recognition template.

INTRODUCTION

Avian brood parasites cause hosts to provide parental care for genetically unrelated young together with or instead of their own offspring (Kilner et al., 2004; Krüger, 2007). Many hosts have evolved strategies to reduce the costs of parasitism (Davies and Brooke, 1988; Takasu et al., 1998; Schulze-Hagen et al., 2009). One of the most prevalent adaptations against brood parasitism is egg rejection, showing individual (Avilés et al., 2009), sex-related (Palomino et al., 1998; Soler et al., 2002; Honza et al., 2007b; Pozgayová et al., 2009), population (Lindholm, 1999; Stokke et al., 2007a) and species-specific variability (Brooke and Davies, 1988; Davies and Brooke, 1989; Moksnes et al., 1991; Røskaft et al., 2002; Servedio and Hauber, 2006). Eggshell characteristics (e.g. coloration and maculation) play a critical role in the recognition of parasitic eggs by hosts of several brood parasite species, including the common cuckoo *Cuculus canorus* (e.g. Nakamura et al., 1998; Stokke et al., 1999; Cherry et al., 2007a; Honza et al., 2007a; Polaciková et al., 2007; Moskát et al., 2008a; Moskát et al., 2008c), the little and Himalayan cuckoos *Cuculus poliocephalus* and *Cuculus saturatus* (Higuchi, 1989), the great spotted cuckoo *Clamator glandarius* (e.g. Soler et al., 2000) and the brown-headed cowbird *Molothrus ater* (e.g. Rothstein, 1982; Underwood and Sealy, 2006). Cognitive mechanisms which correspond to context-dependent egg discrimination (Rothstein, 1975; Welbergen et al., 2001; Lahti and Lahti, 2002; Hauber et al., 2006; Moskát and Hauber, 2007), including the avian-specific sensory perception of egg coloration (Avilés, 2008; Cassey et al., 2008a; Cassey et al.,

2008b; Safran and Vitousek, 2008; Langmore et al., 2009), seem to be key factors in explaining behavioural variability of rejection decisions in host–brood parasite co-evolution. Nonetheless, the extent to which variability in the host's flexibility of species-recognition systems impacts on adaptive responses to parasitism (Sherman et al., 1997; McLean and Maloney, 1998; Stokke et al., 2005; Hauber et al., 2006; Moskát and Hauber, 2007) remains to be fully understood.

Egg discrimination is a prominent antiparasite defence mechanism, implying the successful recognition of the foreign eggs followed by the behavioural decision of the hosts to reject them (Davies and Brooke, 1989; Moksnes et al., 1991; Hauber and Sherman, 2001; Moskát and Hauber, 2007), even in conspecific parasitism (e.g. Jamieson et al., 2000). The two most prevalent mechanisms for egg recognition (Rothstein, 1974; Lahti and Lahti, 2002; Moskát et al., 2009) are (i) discordancy and (ii) recognition from template (Table 1). The latter mechanism requires knowledge of the appearance of the host's own eggs and has been termed 'true recognition' (Hauber and Sherman, 2001) because it requires neural encoding of the recognition template of own eggs. Rejection from template does not require the presence of host and parasite eggs at the same time (Moskát and Hauber, 2007).

Discordancy is the simplest mechanism for egg recognition, and is based on the differences between egg phenotypes within the same clutch (Rothstein, 1974). This mechanism predicts that hosts typically eject the egg types that are most dissimilar (and thus,

Table 1. Examples of egg recognition methods used by hosts in interspecific brood parasitism, as revealed by previous studies

Host	Brood parasite	Reference
Discordancy ¹		
<i>Phylloscopus humei</i>	<i>Cuculus poliocephalus</i>	Marchetti, 2000
<i>Sylvia borin</i>	<i>Cuculus canorus</i>	Rensch, 1925
Recognition template		
<i>Dumetella carolinensis</i>	<i>Molothrus ater</i>	Rothstein, 1974; Rothstein, 1975; Strausberger and Rothstein, 2009
<i>Icterus galbula</i>	<i>Molothrus ater</i>	Rothstein, 1978; Strausberger and Rothstein, 2009
<i>Toxostoma rufum</i>	<i>Molothrus ater</i>	Strausberger and Rothstein, 2009
<i>Quiscalus mexicanus</i>	<i>Molothrus ater</i>	Peer and Sealy, 2001
<i>Luscinia svecica</i>	<i>Cuculus canorus</i>	Amundsen et al., 2002
<i>Fringilla coelebs</i> and <i>F. montifringilla</i>	<i>Cuculus canorus</i>	Moksnes, 1992; Vikan et al., 2009
Discordancy and/or template		
<i>Dendroica petechia</i>	<i>Molothrus ater</i>	Sealy, 1995
<i>Turdus migratorius</i>	<i>Molothrus ater</i>	Rothstein, 1982
<i>Acrocephalus orientalis</i> ²	<i>Cuculus canorus</i>	Lotem et al., 1995
<i>Acrocephalus arundinaceus</i>	<i>Cuculus canorus</i>	Cherry et al., 2007a ³ ; Moskát et al., 2009 ³ ; Hauber et al., 2006 ⁴ ; Moskát and Hauber, 2007 ⁴

¹Discordancy has never clearly occurred; some template recognition was expected (cf. Rothstein, 1974).

²Previously considered as *Acrocephalus arundinaceus orientalis*, a subspecies of the great reed warbler.

³Discordancy.

⁴Recognition template.

necessarily, in the minority) in clutches, irrespective of whether these are their own eggs or parasitic eggs.

Another mechanism is recognition from a template. In this scenario, birds compare the characteristics of the eggs with a recognition template, which could be inherited and/or learned (Rothstein, 1974; Moksnes, 1992; Hauber and Sherman, 2001; Hauber et al., 2006; Moskát and Hauber, 2007; Petrie et al., 2009). Young birds might imprint on their own eggs during their first breeding attempts (Rothstein, 1975; Rodríguez-Gironés and Lotem, 1999; Stokke et al., 2007b) by examining the totality of their clutch (Hauber et al., 2004; Hoover et al., 2006), but first-time breeders might also have some knowledge of their eggs even at their first breeding if the template is inherited or if they imprint immediately on the phenotype of their own first-laid egg (Victoria, 1972; Lotem et al., 1995; Amundsen et al., 2002). In these last cases, additional learning throughout the first breeding attempt or later clutches serves as template updating, an adaptive cognitive mechanism (Hauber and Sherman, 2001) to accommodate the individual's changing extended phenotype (i.e. variability of egg appearance throughout the laying cycle). The aim of our study was to test in a parallel set of experiments whether egg discrimination in the great reed warbler *Acrocephalus arundinaceus* L. occurs by the discordancy or the template-based recognition mechanism.

The great reed warbler is a commonly parasitized cuckoo host in Hungary (41–68% parasitism rate) (Moskát et al., 2008b), with parasitism rate mainly dependent on the availability of trees in the close vicinity of the nests, serving as vantage points for the cuckoo (Moskát and Honza, 2000). This host rejects ca. 34% of naturally laid cuckoo eggs by egg ejection (12%), nest desertion (20%) or egg burial (2%) at Apaj, central Hungary (Moskát and Honza, 2002). However, hosts' rejection frequency does not depend on population-specific parasitism rate across the Hungarian Plain, as a consequence of low site fidelity of this host species (Moskát et al., 2008b). In previous experimental studies template-based egg recognition was revealed by Hauber and colleagues (Hauber et al., 2006), including its variant 'the phenotype distribution', in which all host eggs form a compound template of acceptable phenotype variability and hosts adjust rejection thresholds (Reeve, 1989) based on external contexts (Moskát and Hauber, 2007). However, the possibility of egg

discrimination by discordancy was also suggested in this species by Cherry and colleagues (Cherry et al., 2007a) and by Moskát and colleagues (Moskát et al., 2009), while Moskát and Hauber (Moskát and Hauber, 2007) provided experimental evidence for clutch imprinting through a template-updating mechanism. Because the behavioural evidence for hosts' egg-rejection decisions does not always allow distinction between predictions and outcomes of the discordancy *versus* the template recognition mechanisms (Moskát et al., 2008c; Antonov et al., 2009), contemporary experiments are required that specifically aim to contrast the predictions of these alternative cognitive models using the same experimental paradigm.

In this study we set out to investigate alternative cognitive mechanisms of experimentally induced egg discrimination in this host species, contrasting the potential roles of discordancy and the template recognition mechanism (Table 2), as previous studies suggested that great reed warblers use either the discordancy or the template recognition mechanism (see Table 1). To resolve this uncertainty, here we hypothesized (1) that discordancy plays some role, but not an exclusive one, in egg discrimination by great reed warblers. As discordancy means the rejection of the egg type in the minority (*sensu* Rothstein, 1974), it might be maladaptive in a population with heavy multiple cuckoo parasitism, including our Hungarian study site (Moskát et al., 2009). Therefore learning may also be important in egg recognition in great reed warblers (e.g. Rothstein, 1974; Rodríguez-Gironés and Lotem, 1999; Hauber et al., 2006; Stokke et al., 2007b). We hypothesize (2) that hosts' opportunity to inspect and learn the appearance of eggs in a nest helps egg recognition. Accordingly, we predict that hosts that had the opportunity to observe manipulated eggs during the laying process would show fewer rejections of the manipulated egg(s), when the hosts' own eggs are in the minority within the clutch, relative to those hosts with own eggs in the minority without the opportunity to inspect manipulated eggs during laying. Finally, a third factor for self-phenotype recognition is the presence and varying numbers of own eggs during parasitism where female parasites remove hosts' own eggs (Moskát and Hauber, 2007). Accordingly, we hypothesize (3) that the disappearance of hosts' own eggs is a cue for actual and impending parasitism and increases hosts' egg discrimination, because cuckoos predictably remove host

Table 2. Predicted variation in hosts' egg rejection responses according to different hypothetical cognitive mechanisms used for egg discrimination of moderately mimetic parasitic eggs: discordancy (Rothstein, 1974) and recognition template (cf. Hauber et al., 2006)

Treatment	Egg type		Predicted responses of hosts (rejection rates)	
	Minority	Majority	Discordancy	Recognition template
Spotted egg	Spotted	Own	Moderate	Moderate
Negatively spotted egg	Negatively spotted	Own	High	High
All spotted eggs	None	Spotted	None	Moderate*
'Without learning'	Own	Spotted	None	Moderate
'With learning' [†]	Own	Spotted	Moderate	None [‡]

The basic egg type used in the experiments ('spotted egg') had 20 large brown spots painted on the natural eggshell of the host's own egg. (Note that throughout this table we assume that hosts use only one of the recognition mechanisms.) The predicted reactions against hosts' own eggs are shown in parentheses.

*Relatively good mimicry allows hosts to reject the parasitic egg phenotype at a low frequency, but the lack of the own phenotype is expected to increase rejection rates.

[†]The treatment 'with learning' means the false imprinting on the parasitic eggs' phenotype. In the other treatments hosts had the chance to learn their own eggs' phenotypes.

[‡]This may depend on the mechanism by which hosts acquire the recognition template.

eggs prior to or during parasitism (see above). Hosts might use this cue to shift their acceptance thresholds to be more discriminating (Reeve, 1989; Hauber et al., 2006).

In addition, we studied the importance of eggshell pattern in self-phenotype recognition. A recent study by Moskát and colleagues (Moskát et al., 2008c) revealed that experimentally increased spot density had little effect on hosts' egg discrimination up to 75% cover of the eggshell surface, but when no piece of the original was seen, rejection rate abruptly increased to 100%. For this reason we tested how different components of the eggshell pattern (i.e. background colour *versus* maculation) contribute to the recognition (*versus* non-rejection) of the own egg phenotype. Accordingly, we hypothesize (4) that all hosts' own eggs whose background colour is left visible are available for the recognition of own-egg phenotypes and thus are rejected less often than parasitic eggs.

MATERIALS AND METHODS

Study site and species

The study was conducted in the surroundings of the village of Apaj (47°07'N; 19°06'E) in central Hungary, ca. 40–60 km south of Budapest. The study was performed in 2008, from mid-May until mid-June. We did not band individuals for identification in the study site, but pseudoreplication chance is low (Moskát et al., 2009). In this study area great reed warblers are particularly heavily parasitized by cuckoos. For details of the study site and basic methods, see Moskát and Hauber (Moskát and Hauber, 2007). The experiments performed in this study complied with Hungarian laws on the care and use of animals.

We systematically searched for great reed warbler nests in the 2–4 m wide channel-side reedbeds (*Phragmites australis*) once or twice a week. We used nests which were not parasitized by the cuckoo for experiments, and we deleted those nests from the data set which were parasitized during the control period. In Apaj, great reed warblers lay in the early morning, but cuckoos can lay throughout the whole day, with evening laying times more prevalent (C.M., unpublished observations), as observed in other hosts (Wyllie, 1981; Davies and Brooke, 1988; Honza et al., 2002). Cuckoos typically remove one randomly selected host egg from parasitized clutches [0 egg: 8%, typically when cuckoos lay into empty nests; 1 egg: 86%; 2 eggs: 6%; calculation based on Moskát and Honza (Moskát and Honza, 2002)]. For treatments, we manipulated one or more of the hosts' own eggs in a nest, painting dark brown spots (see below) onto the eggshell. We used painted

real eggs, following Honza and Moskát (Honza and Moskát, 2008). The eggs of great reed warblers are suitable for such types of painting experiments because a great reed warbler egg is as large as a cuckoo egg (Török et al., 2004). The mimicry of natural cuckoo eggs is typically good in our study area, both as perceived by humans (Moskát and Honza, 2002) and as scored by spectrophotometry (Cherry et al., 2007a; Cherry et al., 2007b), and hosts accept ca. two-thirds of real cuckoo eggs (Moskát and Honza, 2002). For this reason we chose an egg phenotype for experimental parasitism (except for the 'negatively spotted egg' treatment; see below) that is rejected at a similarly moderate frequency. We compared our experimental results on rejection rates with hosts' responses to cuckoo eggs from our observations of natural parasitism as a reference.

Experimental egg types

Spotted egg

On the day when the fourth host egg was laid (modal clutch size: 5; great reed warblers start incubation just after the penultimate egg is laid) (Moskát et al., 2008b), one egg, chosen randomly, was manipulated by painting 20 large dark brown spots of approximately 3–4 mm diameter on it. Artificial spots covered 40–60% of the whole egg surface (Fig. 1B). For all experiments we used dark brown waterproof fibre pens (Faber-Castel OHP-Plus permanent, size code: 1525; colour code: 78; thickness: M-size). In this category, besides the experiments carried out in 2008 ($N=9$), we also used data from previous years ($N=10$), when 20 large spots of 4–5 mm diameter were marked on the eggshell with the same type of pen (Moskát et al., 2008c), because host reactions did not differ between these sets of manipulations (2/10 and 4/9 rejections, Fisher's exact test, $P=0.350$). The colour of these artificial spots was found to be very similar to the dominant type of natural spots of host eggs in our population regarding avian-visible spectra, when assessed by spectrophotometer (300–700 nm) (Moskát et al., 2008c).

Negatively spotted egg

On the fourth day of laying, instead of painting spots on the fourth great reed warbler egg, it was painted 'negatively': large spots of approximately 3–4 mm diameter were left in the original background colour of the eggshell, but inter-spot areas were painted with the dark brown pen. We used 20 negative spots for this treatment, which covered 40–60% of the whole egg surface (Fig. 1C).

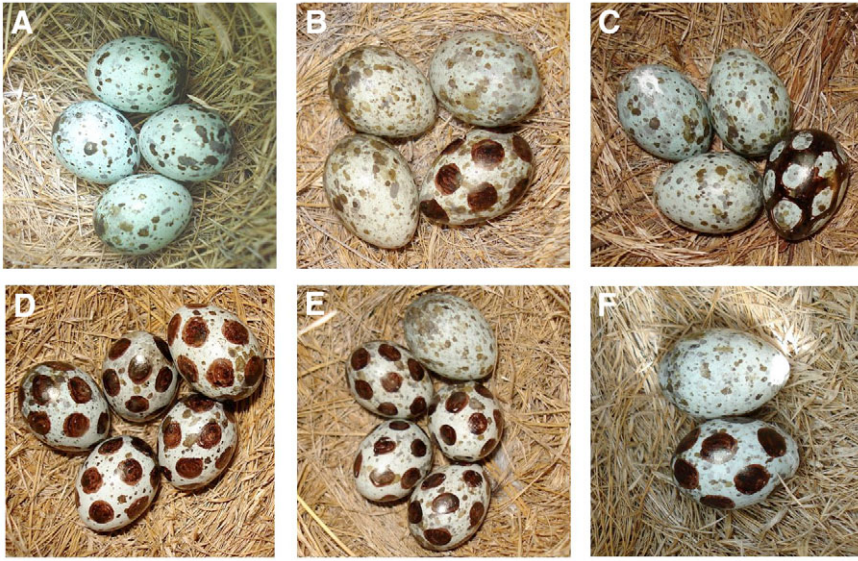


Fig. 1. (A) A non-parasitized great reed warbler clutch ('control'). (B) A great reed warbler clutch with one egg manipulated by adding large brown spots ('spotted egg'). (C) A great reed warbler clutch containing one egg with a painted dark brown background leaving original colour spots ('negatively spotted egg'). (D) All eggs in the clutch manipulated by large brown spots ('all spotted eggs'). (E) All except one egg manipulated by painting large brown spots in the discordancy experiments ('without learning'; see Materials and methods for details). (F) A variant of the 'without learning' case ('with learning') where host had the chance of observing the egg type manipulated by the researcher in which the new egg is painted each day in the early morning. The picture shows one brown spotted egg from the previous day and a new natural egg, which is waiting to be manipulated. (Photo credit: István Zsoldos.)

All spotted eggs

On the fourth day of laying, all four host eggs were painted with 20 large brown spots as for the 'spotted egg' treatment, above (Fig. 1D).

All spotted eggs except one, 'without learning'

Three randomly chosen host eggs were painted with 20 large brown spots at the same time on the fourth day of laying, except one, which was handled but not painted (Fig. 1E).

All spotted eggs except one, 'with learning'

We manipulated newly laid host eggs by painting them with 20 large brown spots (see above; Fig. 1F) each day in the early morning to give hosts the chance to observe the manipulated egg as their own egg. However, we did not manipulate the fourth egg, and typically removed it between 05:30 and 06:30 h local time. In three cases the females laid later, so we checked these nests every 20–30 min until the new egg was laid (not later than 08:00 h). After 3 h we returned this non-manipulated fourth egg to the nest. In this category hosts had the chance to imprint the manipulated phenotype as their own, while in all of the other categories hosts could observe their own egg phenotype following egg laying.

Control

No egg was manipulated, but nest contents were monitored as for the treatments described above (Fig. 1A). We increased the sample size of both controls and the 'spotted egg' treatment using previous years' data sets [$N=13$ in 2008, and $N=12$ from Moskát et al. (Moskát et al., 2008c); with no egg rejected in any subset of the controls, Fisher's exact test, $P=1.000$].

If the host laid one more egg after manipulation at the four-egg state, we left the new (fifth) egg unmanipulated in treatments 'spotted egg' and 'negatively spotted egg', or manipulated by addition of 20 spots for treatments 'all spotted eggs', 'without learning' and 'with learning'. We started experiments with a clutch size of four, for the reason that birds started to incubate clutches just after the fourth egg was laid. At 48 nests (69%) females continued laying to 5 eggs (45 nests) or 6 eggs (3 nests). However, hosts' responses did not differ depending on maximum clutch size (Fisher's exact tests, two-tailed: spotted eggs: $P=0.617$; negatively spotted eggs: $P=1.000$; all spotted eggs: $P=1.000$; all spotted eggs except one

(combined): $P=0.303$). As we did not detect a significant difference when clutches where host females stopped laying just after the fourth eggs were compared with clutches where females continued laying in all of the categories, the number of untreated eggs in clutches did not influence hosts' decisions in response to parasitism.

We monitored nests for 6 days after the fourth day of laying to reveal hosts' reactions, and scored responses as: no response (acceptance) or rejection (egg ejection or nest desertion), following Moksnes and colleagues (Moksnes et al., 1991). This period of monitoring was justified by our previous studies on this host species, where latency of rejection was 1–5 days for each type of parasitic egg: for real cuckoo eggs in natural parasitism (Moskát and Hauber, 2007), and plastic model cuckoo eggs and painted great reed warbler eggs in experimental parasitism (e.g. Honza and Moskát, 2008).

Statistical analyses

We used binary logistic regression analyses for evaluation of the effects of our experiments on the dependent variable (acceptance versus rejection). We treated each experiment as an independent data point, even though hosts were not colour banded [see Moskát et al. for justification (Moskát et al., 2009)], and also because only a single observation or experiment was recorded from each territory, with breeding philopatry also generally low in this population (Moskát et al., 2008b), thereby limiting the possibility of pseudoreplication. For the sake of avoiding the use of two nests of a pair in the season, we did not use replacement clutches in the territory where the first nest failed. We also avoided the use of late nests in the season, which to our knowledge were either replacement clutches or second broods (Moskát et al., 2008b). We included experimental treatment as an independent fixed factor. We also introduced clutch size and egg-laying date in our analyses. This is justified by clutch size being a trait related to the age of the host parent in the great reed warbler, with young females often having smaller clutches than older ones (Bensch, 1996). We entered laying date (laying of the first egg) as a covariate as younger breeding great reed warbler females often lay in the middle of the breeding season, as revealed in the oriental reed warbler (*Acrocephalus orientalis*) in Japan (Lotem et al., 1992) (previously considered as a subspecies of the great reed warbler) (Leisler et al., 1997; Helbig and Seibold, 1999). However, seasonal effects on rejection had not been shown previously at our site (e.g. Moskát and Hauber, 2007;

Moskát et al., 2008a). We also included year as a covariate. Treatment, clutch size and year were used as categorical variables in the analysis, and the option 'backward conditional' was chosen for the selection of covariates.

All statistical analyses were carried out using the program SPSS version 9 (SPSS Inc., Chicago, IL, USA).

RESULTS

Altogether 71 experiments were conducted with known outcomes (i.e. not depredated, parasitized naturally by common cuckoos, or destroyed by storms until response and/or 6 days post-experiment) (Table 3). Rejection rates of the manipulated eggs in the different treatments varied between 25% and 85% (Fig. 2). In the binary logistic regression models, year was not significantly related to rejection rates ($P=0.397$) and was removed at step 2. Laying date ($P=0.377$) was also removed from the model at step 3. In the final model, treatment showed a significant relationship with host responses to parasitism (acceptance/rejection) (Wald=10.09, d.f.=4, $P=0.039$).

Specifically, among the treatments, only the 'negatively spotted egg' was significant in the model (Wald=8.27, d.f.=1, $P=0.004$). The rejection rate of manipulated eggs in this treatment was the highest, as 11/13 of the negatively spotted eggs were rejected by the hosts. Although clutch size was also retained in the model, this covariate was not statistically significant (Wald=6.72, d.f.=3, $P=0.081$). The discriminatory ability of the model was 73%, indicating a good predictive power. The Hosmer and Lemeshow goodness-of-fit test ($\chi^2=2.36$, d.f.=8, $P=0.968$) corresponds to the conclusion that there is an adequate fit of the data to the model. In the model the spotted egg treatment was used as the reference category, where hosts showed moderate rejection rate of the manipulated eggs (6/19 nests). In contrast, the rejection rate was greater in the negatively spotted egg treatment (11/13), which was highly significant (see above). Rejection rates of manipulated eggs in any other treatment (Fig. 2) did not differ from the reference category (rejections in 3/9, 4/16 and 4/14 nests in the 'all spotted eggs', 'without learning' and 'with learning' treatments, respectively, which did not enter as significant in the model, with corresponding P -values of 0.451, 0.733 and 0.295).

Our experiments started on the day when the fourth eggs were laid in the clutches. However, in the 'with learning' experiment hosts were confronted with the manipulated (spotted) egg type every day before this stage during the laying period, i.e. clutches with one,

two or three eggs. This meant that hosts had the chance to reject any of the spotted eggs in this pre-experimental period. We found that hosts rejected at least one spotted egg from 33% of the nests in this period (6/18 versus 4/14 rejections in the experimental period). When we compared all rejections of manipulated eggs (10/18) in the 'with learning' treatments with rejections in the 'without learning' treatment (4/16), the difference was not significant (Fisher's exact test, two-tailed, $P=0.092$).

We documented no ejection costs or rejection errors (i.e. rejection of own eggs) (*sensu* Stokke et al., 2002) in most of the treatments, except in the 'without learning' and 'with learning' treatment. In the 'without learning' treatment we found one nest out of 16 where the host's own egg was ejected with no ejection of any spotted egg (rejection error). In the 'with learning' treatment we also found rejection error in one nest out of 14, and in two nests one or two spotted eggs were successfully ejected together with a host egg (rejection cost). We recorded the loss of 8 spotted eggs during the laying process from 6 out of 18 nests (one egg in 5 nests and 3 eggs in one nest). The number of nests where rejection cost or rejection error occurred did not differ between the 'without learning' and 'with learning' treatments (Fisher's exact test, two-tailed, $P=0.604$).

DISCUSSION

Regarding our first hypothesis, these results provide evidence against a general rule of thumb of discordancy in great reed warblers' egg discrimination of foreign eggs. A few hosts appeared to apply a discordancy mechanism for egg rejection, even though it would be maladaptive for hosts, which use this mechanism in areas where there are high rates of multiple parasitism, as is typical in our population (see above), because hosts would end up rejecting their own eggs once these became the minority in the parasitized clutch. Nevertheless, our results suggest that discordancy is a constituent of the cognitive repertoire of some rejecter great reed warblers which can use it to reduce or escape the costs of cuckoo parasitism. Specifically, hosts in our experiments rejected a few of their own eggs above control levels when they were in the minority in both the 'without learning' and 'with learning' treatments (Table 3).

Our second hypothesis tested the importance of observational inspection of hosts' eggs during egg laying in egg discrimination by the great reed warbler, by exposing hosts to false learning of the parasitic eggs (Strausberger and Rothstein, 2009). We found consistently similar results in the 'without learning' and 'with learning' variants of the 'all spotted eggs except one' treatment as

Table 3. Great reed warblers' responses to manipulated and unmanipulated own eggs

Treatment	Egg in the minority			Eggs in the majority			N
	Egg type	Acceptance	Ejection+desertion	Egg type	Acceptance	Ejection+desertion	
Spotted egg	Spotted	13 (68%)	6+0	Natural	19 (100%)	0+0	19
Negatively spotted egg	Negatively spotted	2 (15%)	11+0	Natural	13 (100%)	0+0	13
All spotted eggs	None	–	–	Spotted	6 (67%)	3*+0	9
'Without learning'	Natural	14 (88%)	1+1	Spotted	12 (75%)	3†+1	16
'With learning'	Natural	12 (86%)	2+0	Spotted	10 (71%)	4‡+0	14
Control	None	–	–	Natural	25 (100%)	0+0	25

Data are number of nests (N).

'Egg in the minority', one egg, natural or manipulated, representing a different phenotype from the dominant egg type in the clutch (*sensu* Rothstein, 1974);

'eggs in the majority', the dominant egg type, natural or manipulated, in the clutch. (Frequency of acceptance is also shown as a percentage.)

*In each of 2 nests, 1 egg was ejected and 2 eggs in 1 nest were also rejected. In 2 out of these 3 cases hosts abandoned their nest after the successful ejection.

†In each of 2 nests, where the unmanipulated egg was accepted, all other (manipulated) eggs were ejected, i.e. 4 or 3 eggs. In 1 nest 1 spotted egg was ejected.

‡In each of 2 nests, 1 spotted egg was ejected. Two eggs in 1 nest and 3 eggs in 1 nest were also ejected.

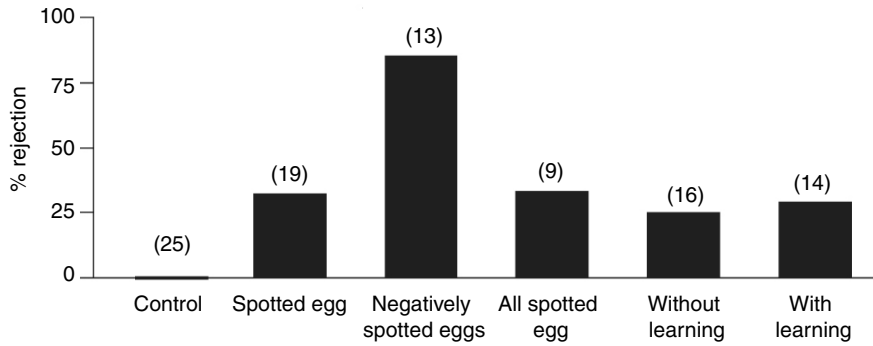


Fig. 2. Rate of rejection by great reed warbler hosts of manipulated own eggs in different treatments, within the 6 day control period following the laying of the fourth egg.

predicted (Table 2). Accordingly, these series of experiments did not support the scenario that this type of clutch inspection (*sensu* Hauber et al., 2004) contributes to rejection decisions in the great reed warbler.

Several types of learning may take place in hosts' behaviour, including learning their own eggs during their first breeding attempt (e.g. Rodríguez-Gironés and Lotem, 1999; Stokke et al., 2007b), learning of own eggs during egg laying (e.g. Rothstein, 1974; Moskát and Hauber, 2007), or learning of the parasite eggs (Hauber et al., 2006). Hosts may also inherit some kind of knowledge of their own egg template (Lotem et al., 1995; Hauber and Sherman, 2001). Prior experience-based recognition templates [e.g. during prior breeding attempts (Lotem et al., 1995) or during juvenile nest prospecting (Safran, 2004)] and inherited templates could both explain why 'learning' (inspecting hosts' manipulated eggs just after they were laid) did not increase tolerance of the manipulated (spotted) eggs, as we predicted. We explain it by the importance of a template recognition-based mechanism. Although learning of the own phenotype during egg laying may contribute to correction of the recognition template (Hauber and Sherman, 2001), this process cannot be prevalent in our great reed warbler populations, where cuckoo parasitism is high and cuckoos frequently parasitize host nests just before hosts have started egg laying (Moskát and Honza, 2002). Otherwise hosts may memorize the foreign cuckoo egg as their own, especially during their first breeding attempts, when they are confronted with eggs in their nests for the first time (Lotem et al., 1995; Hauber et al., 2004).

Our results nonetheless support the cognitive scenario that some great reed warblers possess a stored recognition template of acceptable egg phenotypes and reject parasite eggs based on their dissimilarity to the traits of the template. Further research is needed to evaluate whether learning during prospecting successful clutches or imprinting on own eggs by first year breeders really has consequences for egg discrimination for their later years. As an alternative possibility, it also remains to be studied whether the recognition template of the own eggs could be inherited. However, discriminating between these alternatives cannot be addressed by a simple age-specific comparison of rejection rates in the field between first time and experienced breeders, as proposed previously (Lotem et al., 1995). For example, at our Hungarian study site parasitism rates are so high that older breeders may be equally split between prior experience with parasitized *versus* unparasitized broods. Alternatively, even when first-time breeders reject parasitism (Mark and Stutchbury, 1994), inherited templates may not fully explain this own breeding experience-independent process, because many young birds may inspect eggs and nests during their hatch year, thereby potentially both evaluating the success of previous nesting attempts (Boulinier et al., 1996; Safran, 2004) and forming

recognition templates of conspecific eggs. Furthermore, gene-environment interactions are too complicated to enable us to categorize learned or inherited templates (Hauber and Sherman, 2001). Our findings are nonetheless conclusive, suggesting that both discordancy and template-based rejection to occur in great reed warblers, as independent mechanisms of anti-parasite adaptations.

The 'all spotted eggs' experiments revealed that many hosts (33%) were able to reject one or two parasitic eggs from a clutch, but others were not. In this way these results supported our third hypothesis, that the disappearance of hosts' own eggs facilitated foreign egg rejection. However, the manipulation of hosts' own eggs caused only a small shift in egg appearance (cf. the 32% rejection rate towards a manipulated egg in our 'spotted egg' treatment), so our results suggest that some of the hosts might have regarded the manipulated eggs as their own.

We also tested the importance of eggshell colour and maculation pattern in self-phenotype recognition. Maculation on the eggshell surface may enable individual recognition of an egg ('egg signature') (Davies, 2000) especially in species where intraspecific parasitism commonly occurs, with background colour also playing a part in egg signature (e.g. Lahti and Lahti, 2002). In our great reed warbler population background colour has more importance than spottedness in egg recognition (Moskát et al., 2008c). Spottedness proved to be important in intraclutch variation of eggs. An experimental study showed that increased variation of host eggs' spottedness, by painting on different numbers of dots, reduced hosts' efficiency in foreign egg rejection (Moskát et al., 2008a). Other studies revealed the importance of certain wavelength spectra, e.g. the effects of UV (+) and green (-) reflectance in the song thrush *Turdus philomelos* in foreign egg discrimination (Honza et al., 2007a; Cassey et al., 2008b) [for UV see also Honza and Polaciková (Honza and Polaciková, 2008) in the blackcap *Sylvia atricapilla*]. We used 2-tailed tests in our experiments because there is also a record of non-mimetic manipulation being attractive for hosts (Alvarez, 1999).

In contrast to the prediction of our fourth hypothesis, painting to produce 'negative spotting' showed that great reed warblers reacted differently to pattern types of egg markings, when the paint covered the same proportion of the eggshell surface. This is a surprising result because in a previous study we showed that increasing spot density had no effect on rejection rate by hosts, but when the whole eggshell was painted, rejection rate greatly increased (Moskát et al., 2008c). We explain the present result by differences in rejection behaviour with the higher contrast between the overall colour of experimental eggs and nearby non-manipulated own eggs (Fig. 1), supporting the scenario that rejection is based on contrast between different eggs within the clutch (Braa et al., 1992; Moknes, 1992; Procházka and Honza, 2003; Honza et al., 2004). However, both the discordancy and template recognition mechanisms predict

higher rejection rates for the negatively spotted egg type in contrast with the 'spotted egg' treatment (Table 2), so the 'negatively spotted egg' treatment, when it is evaluated alone, is not suitable for determining the exact egg discrimination mechanism.

Our study utilized several different but parallel experiments on great reed warblers' egg discrimination mechanisms to conclude that egg recognition cannot be explained by one single method. These results provide a methodologically uniform reconciliation of the many contrasting results and claims in the published literature on cuckoo hosts' egg-rejection mechanisms. Specifically, the hosts in our experiment clearly applied different cognitive mechanisms underlying recognition for the resulting behavioural patterns of egg discrimination, including the methods of discordancy and one kind of true recognition, i.e. the template-based mechanism. Rejection rates in different experiments implied a similar relative importance of rejection based on discordancy and template-based rejection. These results are thus consistent with those of Lotem and colleagues (Lotem et al., 1995), who suggested that egg discrimination in the oriental reed warblers cannot be explained only by the discordancy theory. Some birds behaved as if they were using a template.

On the one hand, foreign egg discrimination is clearly a complex process, showing variations in mechanism and proximate context-dependent factors influencing behavioural decisions between hosts. On the other hand, it seems to be a general rule that many bird species that discriminate foreign eggs use one or more variants of the true recognition process. Further studies are needed to clarify the relative importance of discordancy and true recognition in different host species. Great reed warblers' variable tolerance of multiple cuckoo eggs with different egg types (Honza and Moskát, 2005; Hauber et al., 2006; Moskát et al., 2009) suggests that the method of egg discrimination, or the efficiency of the method applied, may depend on the type of parasitism (e.g. single *versus* multiple, sequential parasitism, egg mimicry and the variation in the level of mimicry of parasitic eggs within the same clutch). Future research should also concentrate on the different functions of eggshell components in egg discrimination by hosts of brood parasites (e.g. shape, size, UV, spottedness, marking patterns). *Acrocephalus* warblers are good subjects for such studies, as they are parasitized by the cuckoo in many parts of Europe (Cramp, 1992), representing different stages of ongoing co-evolution (Stokke et al., 2008). Overall, our multi-treatment study revealed fine-tuned differences in great reed warblers' perceptual mechanisms. Our predictions for egg discrimination by hosts proved to be useful when different hypotheses were compared. However, we typically recorded lower rejections than expected, because great reed warblers' responses were shared between the discordancy and the recognition from template model. That is, about half of the great reed warblers, which rejected the parasitic eggs, applied the discordancy method for the recognition of the parasitic eggs, but rejections by others were based on templates.

Data on egg discrimination in hosts of brood parasites suggest that discordancy is the simplest method for egg discrimination (Rothstein, 1974; Marchetti, 2000), which could be used for recognition of brood parasite eggs when mimicry of the parasitic egg is poor. When cuckoos evolve better mimicry, template-based recognition probably gives a better chance of more accurate egg discrimination. Accordingly, two host species of the cuckoo which have been abandoned or nearly abandoned by the parasite, the brambling (*Fringilla montifringilla*) and chaffinch (*Fringilla coelebs*), both remain strong rejecters, including of closely mimetic eggs, through the use of a template-based discrimination (Vikan et

al., 2009). The presence of the cognitive repertoire of alternative egg recognition methods, as indicated in our study for great reed warblers, probably indicates an intermediate stage in the evolution of antiparasite defences, towards an eventual rejection method solely based on template recognition. We suggest that further studies are needed to test the novel prediction derived here and to describe in more detail the evolutionary stages that hosts may be using to rely on different egg-recognition methods, as a function of mimicry by parasitic eggs, host age and breeding experience.

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