

## Conflict between egg recognition and egg rejection decisions in common cuckoo (*Cuculus canorus*) hosts

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**Abstract** Common cuckoos (*Cuculus canorus*) are obligate brood parasites, laying eggs into nests of small songbirds. The cuckoo hatchling evicts all eggs and young from a nest, eliminating hosts' breeding success. Despite the consistently high costs of parasitism by common cuckoos, great reed warbler (*Acrocephalus arundinaceus*) hosts sometime accept and other times reject parasitic eggs. To explore the cognitive basis of this seemingly maladaptive variation in host responses, we documented differences in egg rejection rates within 1-day periods just before and during the egg-laying cycle across host nests. Hosts rejected cuckoo eggs at 28% of nests during the pre-egg-laying stage, but when cuckoos exchanged the first host egg with the parasite egg, rejections increased to 75%. Even later, when several host eggs remained in a nest after parasitism, rejection rate fell to 37.5%. Experimental parasitism with conspecific eggs on the first and second day of host laying showed a similar directional change in relative rejection rates, dropping from 35 to 0%. Mistakes in egg discrimination (ejection error and ejection cost) were observed mostly in the latter part of the laying cycle, mainly when nests contained 5–6 eggs. These correlational and experimental patterns of egg rejection support a cognitive process of egg discrimination

through several shifts in hosts' optimal acceptance thresholds of foreign eggs. The results are also consistent with the evolution of foreign egg rejection in the context of nest-sanitation (i.e. the removal of foreign objects). Our results suggest that common cuckoo hosts may recognize more eggs than they reject. This implies that the experience of the host with one or more of its own eggs in the clutch is a key factor in rejecting parasite eggs by allowing inspection and learning about their own clutch.

**Keywords** Brood parasitism · Egg discrimination · Decision-making · Recognition system · Learning

### Introduction

In obligate avian brood parasitism hosts are exploited by other bird species through parental care for genetically unrelated young (Davies 2000; Krüger and Davies 2002; Payne 2005; Parejo and Avilés 2007). Many hosts of diverse parasite species evolved antiparasite defense mechanisms that help to escape or reduce the cost of parasitism, e.g. through the ejection of the parasitic egg or the desertion of the parasitized clutch or brood (e.g. Davies and Brooke 1989; Moksnes et al. 1990; Davies 2000; Grim et al. 2003; Langmore et al. 2003). Yet, both between and within host species there is much variation in the form and extent of antiparasite rejection behaviors: who, when, and how to reject parasite eggs and chicks (Davies 2000; Avilés et al. 2005; Moskát 2005; Grim 2006; Servedio and Hauber 2006). Understanding the perceptual processes of the hosts that lead to the rejection of parasite eggs is critical in exploring the cognitive basis and the evolution of the

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flexibility of hosts' species-recognition systems (Sherman et al. 1997; McLean and Maloney 1998; Stokke et al. 2005; Hauber et al. 2006).

Egg discrimination in cuckoo hosts depends on the evolutionary history of hosts' adaptations to parasitism (Langmore et al. 2005), and as such it is likely to have a genetic basis (Martín-Gálvez et al. 2006). In turn, the extent of mimicry between host and parasite eggs depends on both the perceptual sensitivity of the host (Holen and Johnston 2004) and the costs of the discrimination process and the rejection decision (Reeve 1989; Davies et al. 1996). Finally, several observations and theoretical models suggest that hosts' egg rejection behaviour also has a conditional process component, depending on the population-level parasitism rate and the risk experienced by individual hosts (Øien et al. 1999; Rodríguez-Gironés and Lotem 1999; Avilés et al. 2005; Holen and Johnston 2006; Servedio and Hauber 2006). Consequently, hosts may recognize more eggs than they reject (e.g. Rothstein 1975, 1977, 1982a, b), leading to seemingly maladaptive decisions (Holen and Johnstone 2004), especially when acceptance of parasite eggs leads to total reproductive failure of hosts' breeding attempts. In the absence of direct evidence for neural mechanisms of sensory perception of parasite eggs (Hauber and Sherman 2001), most behavioral discrimination studies generally focus on the action response, rather than on the perception component of recognition systems (Liebert and Starks 2004; Mateo 2004). Previous field and experimental studies in avian brood parasitism were not able to distinguish between recognition and rejection, combining the perceptual and action components of host recognition systems under the term egg discrimination. For instance, pecking of the parasitic egg by puncture ejector host species prior to ejection implies recognition (Soler et al. 2002), and others, e.g. the grasp ejector kurrichane thrush (*Turdus libonyana*), recognized and rejected the parasitic eggs with short latencies (Honza et al. 2005), implying recognition in concurrence with the antiparasite response action.

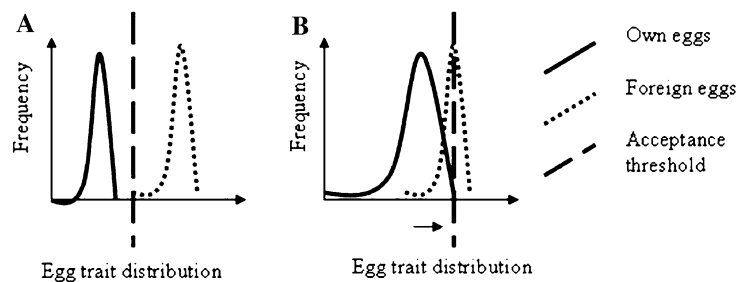
Prevailing theories suggest that hosts can use at least two alternative cognitive mechanisms in egg recognition. A direct comparison of eggs in the clutch assumes that hosts compare their own eggs with the parasitic egg and reject the dissimilar outlier (Marchetti 2000; Hauber and Sherman 2001; Servedio and Lande 2003). But there are only a handful of studies, which supported this idea; for instance, Rensch (1925) found that garden warblers (*Sylvia borin*) accepted lesser white-throat (*Sylvia curruca*) eggs when complete clutches were exchanged, but rejected their own eggs if they were laid later. Similar results were reported by Rothstein (1974) working with gray catbirds (*Dumetella*

*carolinensis*) and Victoria (1972) working with village weavers (*Ploceus cucullatus*). According to this clutch-learning scenario, hosts memorize the appearance of their own eggs on each day of egg-laying, and consequently, they show greater tolerance towards the parasite eggs in the early stages of their breeding cycle than after clutch completion. False imprinting of foreign eggs during egg laying might lead to incorrect recognition of hosts' own eggs (Hauber et al. 2004; Hoover et al. 2006). Such patterns of own-egg rejection would be considered the result of an ontogenetic learning process, rather than the outcome of a decision rule to reject eggs that differ from the majority (rejection by discordancy) (Rothstein 1974).

In contrast, other hosts may use a memory-based cognitive template of their own eggs (Moksnes 1992; Hauber and Sherman 2001; Hauber et al. 2006). Although this template might be inherited (e.g. Amundsen et al. 2002; Stokke et al. 2004), observational learning (Lotem et al. 1995) may contribute to the formation of the recognition template of hosts' own eggs. All these different ontogenies and mechanisms in avian egg recognition systems are not necessarily mutually exclusive, as was reported for gray catbirds (Rothstein 1974), which primarily use the method of direct comparison in egg recognition but also learn and remember aspects of their own eggs (see above).

A little explored variant of the second mechanism of egg recognition is clutch assessment through template updating. According to this mechanism, hosts use the appearance of the eggs laid by themselves to determine the trait distribution of their own eggs and to discriminate foreign eggs whose appearance falls outside this distribution (Servedio and Lande 2003), following a decision rule shaped by flexible optimal acceptance thresholds (Reeve 1989; Davies et al. 1996; Hauber et al. 2006; Holen and Johnstone 2006). Under this scenario, the more eggs a female lays, the greater the perceived phenotypic variability of her own eggs will be. The widening trait distribution of her own eggs will in turn mean that foreign eggs will be more likely to fall within this widening trait distribution and thus will be more likely to be accepted (Fig. 1).

While the perceptual component of recognition systems can take place by comparing current eggs within a clutch or by acquiring the recognition template through experience, the action component of rejection decisions is strongly influenced by the extent of mimetic similarity of the parasite egg to the host egg (sensu Grim 2005), typically with more accurately mimetic eggs being rejected at lower rates (e.g. Davies and Brooke 1989; Moksnes et al. 1990; Welbergen et al. 2001; Bártol et al. 2002; Moskát and Honza 2002;



**Fig. 1** Relative distribution of phenotypic traits of host eggs and cuckoo eggs based on a clutch-inspection learning mechanisms to form recognition templates at **a** one-host-egg stage and **b** multiple-

host-egg stage. The optimal acceptance threshold (Reeve 1989) shifts to the more permissive range with increasing host egg numbers

**Table 1** Variation in hosts' egg rejection responses across different laying stages (pre-egg-laying, one-host-egg and multi-host-egg stages, i.e. 0, 1 and 2–5 host eggs, respectively), as predicted by different cognitive mechanisms used for egg discrimination

Stage of laying	Variation in rejection rate with different cognitive mechanisms			
	1. Direct comparison	2. Memory template	3. Phenotype distribution	4. Onset of laying
Pre-egg-laying	Low	High	Low	High
One-host egg <sup>a</sup>	Low	High	High	Low
Multi-host-egg	High	High	Low	Low

<sup>a</sup> In natural cuckoo parasitism cuckoos usually remove one host egg when parasitizing hosts' clutches, so no host egg remains in the nest in this category once parasitism occurs

Soler et al. 2003; Avilés et al. 2004; Honza et al. 2004; Antonov et al. 2006; Cherry et al. 2007a). Non-mimetic patterns of parasite eggs may not always increase rejection rate, but could also serve as attractive stimuli for hosts (Alvarez 1999). Finally, rejection decisions may be influenced by the various costs of antiparasite strategies and tactics. During the attempt to reject parasitism hosts may accidentally damage their own eggs or eject own eggs or abandon their own non-parasitized clutches (Davies 2000). The neural basis underlying cognitive processes of template memorization and acceptance threshold shifts may also provide significant energetic and temporal costs (Lotem 1993). How these different cognitive mechanisms and fitness costs contribute to contrasting patterns of perception and action remain unclear for most host-parasite systems (Davies 2000).

In this study, we compared frequencies of rejection of parasite eggs by great reed warbler (*Acrocephalus arundinaceus*) hosts of the common cuckoo (*Cuculus canorus*), across consecutive laying stages at the beginning of the breeding cycle. We set out to compare predictions of different recognition mechanisms involved in hosts' rejection decisions in the context of natural cuckoo parasitism (Table 1). If hosts used a direct comparison (1) between own and parasite eggs to recognize and reject parasite eggs, we predicted low rejection rates of cuckoo eggs during the pre-laying stage and on

the day when the first host egg is exchanged by the cuckoo for a parasite egg. In contrast, we predicted high rejection rates during the later stages of the laying cycle when parasite and host eggs are found together in host nests. Alternatively, if hosts used a memory-based template (2) to recognize parasite eggs, we predicted high rates of rejection irrespective of the stage of the laying cycle. Further, if hosts used the phenotype distribution of their own eggs (3) to discriminate parasite eggs, we predicted a low rejection rate of parasite eggs during mid- and late egg-laying stages (when host eggs are present) and during the pre-laying stage (when hosts eggs are absent). In contrast, we predicted higher rejection rates when only one host egg had been laid and replaced by a cuckoo egg. Finally, if hosts use a decision mechanism to reject all eggs that are laid in nests prior to the onset of their own laying (4) (e.g. acorn woodpeckers *Melanerpes formicivorus*: Koenig and Mumme 1987; yellow warblers *Dendroica petechia*: Sealy 1995), we predicted high rejection rates in the pre-egg laying stage, and lower rejection rates during the remainder of laying stages.

## Methods

The study was conducted in the Hungarian Great Plain, ca. 50 km south of Budapest, in the 20 km radius

of Apaj (47°07'N, 19°05'E). Great reed warblers at this site breed in 2–4 m wide strips of reeds (*Phragmites australis*) along both sides of small channels. Our host population suffers from an unusually high frequency of cuckoo parasitism (ca. 64%) and hosts show a moderate level of antiparasite defense against naturally laid cuckoo eggs (overall rate of rejecting cuckoo eggs is ~34%; Moskát and Honza 2002). Earlier studies based on color banding revealed negligible phylopatry of adult birds (i.e. reducing the chance of pseudoreplication across years), no site fidelity for juveniles at the geographic scale of our study area, and great reed warbler populations across the Hungarian Great Plains and in Transdanubia, Hungary, show similar rejection rates, reproductive success, and genetic structure (C. Moskát, B. Hansson, L. Barabás, I. Bártol, Z. Karcza and T. Kisbenedek unpublished data).

Field work was conducted from 1998 to 2005, between mid-May to late June or early July. We searched for new nests in sections of channels at least two times a week, and nests were checked daily, generally in the morning. In this population hosts lay in early morning, cuckoos can lay all day, but typically in the evening (C. Moskát, unpubl.), and cuckoos typically remove one randomly selected egg when laying their own eggs (0 egg: 8%, 1 egg: 86%, 2 eggs: 6%; calculation based on Moskát and Honza 2002). Hosts' responses were categorized as acceptance, ejection and burial of the parasite egg, or desertion of the parasitized nest (see Moskát and Honza 2002 for further details).

To explore the cognitive context of the variation in hosts' rejection decision, we divided naturally parasitized hosts into three separate groups. PRE-EGG-LAYING stage (i): we examined rejection rates of hosts that received cuckoo eggs prior to the onset of the host's laying period (mean =  $1.25 \pm 0.55$  SD days before hosts' laying started). This means that the cuckoo egg appeared in the host nest in the absence of any warbler egg. ONE-HOST-EGG stage (ii): we examined hosts whose first-laid egg was removed and replaced by a cuckoo egg on the first day of the laying period. This means that the host had the opportunity to inspect its own egg but at the time of the potential discrimination decision the cuckoo egg again was the only egg in the nest after parasitism. MULTI-HOST-EGG stage (iii): we examined hosts that received cuckoo eggs further into the laying period, when two or more of their own eggs were already laid, so nests contained both warbler and cuckoo eggs.

A portion of the nests, not parasitized naturally by cuckoos, was assigned to experimental treatments in 2001 to explore the hosts' fine-tuned reactions to accu-

rately mimetic parasite eggs. We used foreign conspecific eggs to simulate parasitism by highly mimetic cuckoo eggs, because the mimicry of the eggs of 'great reed warbler' cuckoos in Hungary is typically good (Southern 1954; Moskát and Honza 2002). Although some cuckoo eggs seem to be indistinguishable from host eggs for humans (Moskát and Honza 2002; C. Moskát unpublished), the average mimicry of cuckoo eggs in a population is expected not to reach the level of foreign conspecific eggs (Lovász and Moskát 2004). Experiments were carried out during the (ii) one-host-egg and (iii) multi-host-egg stages by exchanging one host egg with a conspecific egg. In the latter category clutch size always was two when the experiment started, so that this category should be considered a subset of the multiple-host-stage (iii). An earlier study in our study area revealed that great reed warblers are able to reject only a small portion of experimentally introduced conspecific eggs during the egg-laying stage when clutches contained four host eggs (12.5%; Bártol et al. 2002).

Because mistakenly ejected own eggs during ejection of the parasite egg may reveal some important characteristics in hosts' egg discrimination (Davies and Brooke 1988; Marchetti 1992), we also examined these events, using the following definitions based on Røskft et al. (2002) and Stokke et al. (2002): *ejection cost*—breakage of host's own egg(s) during ejection of the parasitic egg, *ejection error*—ejection of host's own egg(s) without any harm to the parasitic egg, and *recognition error*—ejection of a host's own egg in an unparasitized nest.

Statistical analyses were carried out by STATISTICA 5.0, and all tests reported are two-tailed. Global analyses of the data were based on a generalized linear model approach in SPSS 12.0. Our model selection used rejection or acceptance as a binary dependent variable ("response") with the inclusion of the following fixed factors: "nesting stage" (0, 1, 2–5 host eggs) and "egg-type" (natural cuckoo vs. conspecific). As individual hosts' responses may show seasonally variable patterns (Lotem et al. 1992), we added "season" (laying date) as a covariate, and "year" as a random factor. Laying dates started within a narrow range of calendar days in different years, between May 9 and May 12, regarding all nests of great reed warblers found (C. Moskát, unpubl.), and for analyses were standardized by assigning day 1 for the earliest day of laying onset in each year. Post-hoc univariate comparisons were conducted to detect patterns of variation of antiparasite responses between different laying stages of hosts and between observational and experimental results.

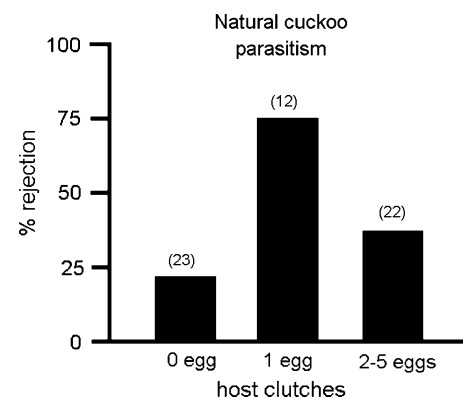
## Results

The generalized linear model revealed that rejection of parasitic eggs was influenced by the nesting stage ( $F = 7.690$ ,  $df = 2.78$ ,  $P = 0.001$ ). Thus, hosts' responses towards either natural cuckoo eggs or experimental conspecific eggs were only affected by the number of host eggs already laid in the nest (0, 1, or 2–5). We detected no variation in responses according to season of laying date (mean  $\pm$  SD =  $17.00 \pm 10.01$ ;  $F = 0.050$ ,  $df = 1.78$ ,  $P = 0.823$ ), year ( $F = 1.099$ ,  $df = 7.78$ ,  $P = 0.372$ ) or parasite egg-type (natural cuckoo vs. experimental conspecific eggs;  $F = 2.381$ ,  $df = 1.78$ ,  $P = 0.127$ ). The lack of seasonal effect of laying date implies that age differences between earlier and later nesting female great reed warbler hosts (cf. Lotem et al. 1992) did not explain the observed variation in rejection rates.

In the case of naturally laid cuckoo eggs great reed warblers rejected these at variable rates that consistently differed between the laying stages of their own clutch (Kruskal–Wallis  $H = 10.593$ ,  $df = 2$ ,  $n = 57$ ,  $P = 0.005$ ) (Fig. 2). When the nest was parasitized in the pre-egg-laying stage (i) 21.7% (5/23; 2 ejections, 2 desertions and 1 egg burial) of naturally laid parasite eggs were rejected. The latency until rejection was 1 day, except for one egg ejection, which was observed after 2 days. In this stage no host eggs appeared in the nests, but one or two days later, hosts normally started egg laying if the cuckoo egg was accepted and thus this subset of hosts continued to accept the cuckoo egg after they began to lay.

Next, rejection rate of cuckoo eggs by great reed warblers abruptly increased to 75% (9/12; 7 desertions, 1 ejection and 1 egg burial) when nests were parasitized in the one-host-egg stage (ii). Eight out of the nine rejections had exact known dates for rejection, and all happened within 1 day. The difference in rejection rates between the pre-egg-laying and the one-host-egg stages is significant (Fisher's test,  $P = 0.004$ ), but latency until rejection (see above) did not differ (Mann–Whitney  $U_{5,8} = 16.000$ ,  $P = 0.558$ ).

Finally, rejection rate decreased to 37.5% (6/22; 5 ejections and 1 desertion) in the multi-host-egg stage (iii). The difference in rejection rate between the one-host-egg and multi-host-egg stages was also significant (Fisher's test,  $P = 0.012$ ), but rejection rate during the multi-host-egg category did not differ from that in the pre-egg-laying stage (Fisher's test,  $P = 0.738$ ). Latency until rejection was also higher in the multi-host-egg stage (iii) than during the earlier stages (i–ii), with mean rejection latencies of 3 days (range: 1–5 days), and rejection latencies differed across the three laying



**Fig. 2** Great reed warbler responses to cuckoo parasitism in relation to number of host eggs when parasitized. (0 egg: 0 host egg and cuckoo laid one parasite egg into the nest (pre-egg-laying stage); 1 egg: 1 host egg was swapped by cuckoo to parasite egg, so no host egg remained in the clutch (one-host-egg stage); 2–5 eggs: nest contained 2–5 host eggs and cuckoo swapped one host egg with a parasite egg (multi-host-eggs stage). (Number of nests is shown in parentheses)

stage categories (Kruskal–Wallis  $H = 10.5$ ,  $n = 18$ ,  $P = 0.005$ ). That hosts rejected the cuckoo egg typically within one day both in the pre-egg-laying (i) and one-host-egg stages (ii) suggests that host eggs laid subsequent to parasitic eggs did not affect hosts' rejection decisions.

Experimental parasitism with highly mimetic eggs (conspecific eggs) showed statistically similar (Fisher's exact tests, two-tailed) rejection rates compared to natural parasitism both when the manipulation was carried out during the one-host-egg stage (ii) (35%; 7/20; three ejections and four desertions, versus 9/12 rejected natural cuckoo eggs,  $P = 0.0659$ ) and during the two-host-egg stage (ii) when no rejection was observed (0/13 vs. 6/22,  $P = 0.0645$ ) (Fig. 3). In addition, the difference in rejection rates of experimental eggs between these laying periods was both significant (Fisher's exact test,  $P = 0.027$ ) and mirrored the relative direction of the difference found in rejection rates between naturally parasitized stage (ii: higher) and (iii: lower) nests. Latency until rejections was again 1 day, except in one case that occurred within 2 days. Thus, the experimental parasitism with conspecific eggs revealed a similar direction of change in host reactions between one-egg and two-host-egg stages as did parasitism by natural cuckoo eggs between one-egg and multi-host-egg stages.

Ejection errors [conceptually equivalent to the 'rejection errors' of Røskoft et al. (2002) and Stokke et al. (2002)] and ejection costs were documented predominantly when clutch sizes were larger (Table 2). Nine cases out of 16 (56%) where ejection error occurred, i.e. the hosts ejected one or more host eggs



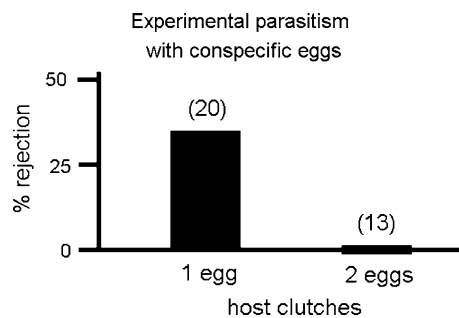
**Table 2** Numbers of ejection errors and ejection costs obtained from great reed warbler nests parasitized by common cuckoos

	Number of host eggs in parasitized nests at the time of egg ejection							N
	1	2	3	4	5	6	un.	
Ejection error <sup>a</sup>	0	1	2	2	2	9	–	161
Ejection cost <sup>b</sup>	0/5	0/3	2/11	1/6	4/5	0/1	0/5	36

Nests in each category contained a cuckoo egg, even in the pre-egg-laying stage (0 host eggs). Note that category 1 host egg contained only a single cuckoo egg and no warbler egg, as cuckoos typically exchange one host egg with their egg when laying. Neither ejection error nor ejection cost may occur when clutches contain only cuckoo eggs [un = unknown; for ejection costs (number of clutches where ejection cost was observed)/(total number of ejections) are presented]

<sup>a</sup> Ejection of host's own egg(s) without any harm to the parasitic egg

<sup>b</sup> Breakage of host's own egg(s) during ejection of the parasitic egg



**Fig. 3** Great reed warbler responses to experimental parasitism by highly mimetic experimental eggs (conspecific eggs) when nests contained one versus two host eggs (1 egg: the first laid host egg was exchanged with a conspecific egg from a different female (one-host-egg stage); 2 eggs: the second host egg was exchanged with a conspecific egg (two-host-egg stage). (Number of nests is shown in parentheses)

but the cuckoo egg remained in the nest, were observed in six-egg clutches (the modal clutch size is five eggs in our population, C. Moskát unpubl.). Also, ejection costs (7 cases out of 36), i.e. when hosts ejected the parasite egg successfully but together with one or more of its own eggs, four out of the seven cases occurred in nests containing five eggs. We observed the disappearance of hosts' own eggs from unparasitized nests (i.e. potential cases of recognition errors) during the multiple host egg stage in this data set ( $n = 40$  nests), when nests had either six eggs or, on two occasions, four eggs.

## Discussion

Observational data during the pre-egg-laying stage indicated that some great reed warbler hosts rejected parasite eggs (Fig. 2). All these individuals could only use an innate or a long-term memory-based template (learned during previous breeding attempts) to discriminate between own and parasite eggs. In contrast, during the one-egg stage birds higher proportions of

hosts rejected cuckoo eggs (Fig. 2). These individuals could use innate templates, memory, or both to recognize foreign eggs once the female cuckoo exchanged her own parasite egg with the host egg. Although we did not test critical predictions to discriminate all possible mechanisms in egg discrimination (see [Introduction](#)), these findings are most consistent with a cognitive mechanism to discriminate cuckoo eggs using a phenotype-distribution based decision rule (3) compared to alternative mechanisms (1, 2, or 4: Table 1).

In the absence of following individual hosts' responses across the laying cycle to repeated parasitism, as shown by Hauber et al. (2006) in the great reed warbler, we cannot discriminate between the possibilities that either (1) individuals modulate their responses to foreign eggs across the subsequent stages of the laying cycle or (2) hosts with different propensities of rejection reach the subsequent stages of the laying cycle with varying likelihood. As the difference between laying categories was typically only one day between laying stages (i) and (ii), and 1–4 days between stages (ii) and (iii), we suggest that option (2) does not explain our results. Irrespective of the cognitive and population-level mechanisms of egg recognition, these results imply that the stage of the laying process and the appearance of hosts' own eggs critically influence whether, and at what frequency, foreign eggs are rejected from host nest.

According to signal detection models of egg rejection (Davies et al. 1996; Rodríguez-Gironés and Lotem 1999), based on optimal acceptance thresholds (Reeve 1989), hosts' decision whether to accept or reject parasite eggs depends mainly on parasitism rate at the specific developmental mode of the hosts' egg discrimination ability. Although our results are qualitatively concordant with patterns of cost-driven optimality in hosts' rejection rates of natural and experimental parasite eggs, it remains to be determined to what extent physiological, sensory, temporal, and ecological constraints influence hosts' actual rates of behavioural

responses to cuckoo parasitism (Waite 2002). For example, why are hosts' rejection rates not the highest against foreign eggs in the pre-egg-laying stage, which is free from ejection cost and ejection error? We explain this with the importance of observational learning and experience of hosts' with their own eggs: the sight of the first host egg in the next stage (the one-host-egg stage) increases hosts' recognition ability. The behavioural decision between the acceptance or rejection of an egg may depend on the rank order of options available to the actor, which in turn may depend on the number and type of eggs in the nest that can be inspected at that time (cf. Bateson and Healy 2005). When ejection is potentially more costly because of the possibility of ejection errors and ejection costs, hosts seem to be less frequently choosing rejection than they are able to recognize the parasitic eggs.

According to the adaptive-choice model by Waite (2002), selection favors minimizing costly errors. Under this scenario, more accurate discrimination is expected when the potential costs of erroneous decisions are greater, as was observed in spatial memory studies in the Clark's nutcracker *Nucifraga columbiana* (Bednekoff and Balda 1997). Our results similarly suggest that in discrimination of parasitic eggs, the hosts seem to decide upon acceptance instead of the costly rejection of mimetic parasite eggs when clutches contain several host eggs. Yet, from the selective context of parasitic egg discrimination, any decision rule that leads to the acceptance of the foreign egg is maladaptive because the parasitic hatchlings evict all host eggs and nestlings and the parents end up rearing only the genetically unrelated cuckoo chick instead of their own offspring. A possible explanation for this evolutionary paradox is that hosts recognize foreign eggs as foreign objects (Moskát et al. 2003), but not as parasitic eggs. Hence, they do not respond to cuckoo eggs in the context of parasitism, and thus pay the severe fitness costs (total breeding failure) of accepting successful parasitism by evictor cuckoos. So cuckoo parasitism seems to be driving hosts' counteradaptation to parasitism by selecting for hosts with better cognitive abilities to recognize traits of own brood (Hauber and Kilner 2007). A prediction of this adaptive cognitive scenario is that seemingly antiparasitic behavioural responses have actually evolved in the context of other life history selection. Accordingly, Bell's vireos (*Vireo bellii*) respond to brood parasitism of brown-headed cowbirds (*Molothrus ater*) by deserting nests, but this is a behavioural decision in response to reduced host clutch sizes when female cowbirds remove host eggs prior to laying and not to the costs of raising parasitic chicks (Kosciuch et al. 2006).

Although eggshell color and pattern of maculation is inherited maternally, and probably W-chromosome linked in passerine birds and their parasites (Gibbs et al. 2000; Gosler et al. 2000), the evolution of host egg appearance may have an additional dynamic aspect (Takasu 2003). Accordingly, when food, climate, host age, and other circumstances influence host egg appearance (Underwood and Sealy 2002, Avilés et al. 2007), one or more eggs in a clutch may deviate in appearance from the others. So the learning component of self-egg recognition systems may have relevant importance in the role of ensuring flexibility of recognition (cf. Rothstein 1974; Soler and Soler 1999; Hauber et al. 2000; Hauber and Sherman 2001).

Moskát (2005) reported that about 36% of all natural cuckoo eggs found in our study area in great reed warbler nests were laid during the combined categories of the pre-egg-laying (i) and one-host-egg stages (ii), with about 1/3 of these cuckoo eggs were laid during the one-host-egg stage. So why do cuckoos not avoid laying in this most costly (i.e. most frequently rejected cuckoo eggs) laying stage? One explanation is that cuckoos visit host nests more often than they lay eggs (Moksnes et al. 2000; Honza et al. 2002; Vogl et al. 2002; 2004) to select nests for better matching of their eggs to host eggs (Avilés et al. 2006; Cherry et al. 2007b). They may also evaluate hosts' parental ability (Parejo and Avilés 2007) based on eavesdropping of heterospecific sexual signals. But cuckoos lay eggs at every second day (Wyllie 1981), and they might be constrained to lay their next eggs into active nests one or two days after discovery (i.e. during the multiple-host-egg stage). Furthermore, cuckoos are also under selection pressure to lay their eggs as early as possible to avoid competition among cuckoo chicks in multiple parasitism (in many cases the earlier-hatched cuckoo chick has the chance to evict the other cuckoo egg(s) before its/their hatching; Davies 2000). Although synchronization of cuckoos with hosts in egg laying reduces multiple parasitism (Moskát et al. 2006), frequency of multiple parasitism is still high in our population with about 36% of the parasitized nests contained 2 or 3 (rarely 4) cuckoo eggs (Moskát and Honza 2002). To evaluate these alternatives will require comparisons of the variation in hosts' rejection rates across the laying cycle and the timing of cuckoos' egg laying across less-intensively parasitized great reed warbler and other host species populations. These comparisons might reveal the potential for co-evolutionary arms races between hosts' cognitive mechanisms to reject costly parasite eggs and the influence of ecological constraints on parasites' decision rules to lay eggs during periods of lower chances of host rejection.

In our experimental parasitism the highly mimetic conspecific eggs were rejected at statistically similar rate to the rate at which the generally highly mimetic cuckoo eggs were rejected following natural parasitism, thus the mimicry effect (cf. Davies 2000) did not mask the consistent effect of number of host eggs on the patterns of rejection rate-variation across two stages (ii vs. iii) of the hosts' laying cycle. There is genotypic variability of individuals to recognize eggs (Lotem and Nakamura 1998; Palomino et al. 1998), recently demonstrated by Martín-Gálvez et al. (2006) for different magpie populations (*Pica pica*), parasitized to varying degrees by the great-spotted cuckoo (*Clamator glandarius*). However, ecological and social factors may have also contributed to individual differences in hosts' phenotypic responses to parasitism found between our natural and experimental parasitism (Holen and Johnstone 2006). Such extrinsic factors might consist of experience with the presence of an adult brood parasite near the nest and overall parasitism rate (Davies and Brooke 1988; Moksnes and Røskaft 1989; Lindholm and Thomas 2000; Bártol et al. 2002) and multiple or repeated parasitism (Orians et al. 1989; Kattan 1997; Palomino et al. 1998; Hauber 2001; Honza and Moskát 2005; Hauber et al. 2006; Hoover et al. 2006). The interaction of ecological opportunity and constraint with perception and cognition should be tested in future studies on host-parasite systems where individually-marked, known-age host subjects can provide sufficiently large sample sizes for experimental parasitism.

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