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Original Article

Closer clutch inspection—quicker egg ejection: timing of host responses toward parasitic eggs

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The prevalent, and so far most explored, host defense against brood parasitism is egg discrimination. Not only do the hosts differ markedly in their propensity to reject parasitic eggs but rejecters even vary in their egg rejection times. The focus of the present study was to investigate factors potentially responsible for high variation in timing of host egg rejection. As a model species, we chose the great reed warbler *Acrocephalus arundinaceus*, a cuckoo *Cuculus canorus* host, with female-restricted egg ejection behavior. We presented a cuckoo dummy near host nests and experimentally parasitized the clutches with a nonmimetic egg. Immediately afterward, we continuously video recorded host behavior to determine egg ejection times accurately. We fitted a regression tree model with the timing of egg ejection as a dependent variable and female-related characteristics (body condition, eggshell coloration, and behavior) as explanatory variables. Only female behavior toward the foreign egg proved to have a significant effect on the timing of egg ejection. Females devoting more time to clutch inspection ejected the egg significantly more quickly than females inspecting their experimentally parasitized clutches only briefly. We discuss our results in the context of known intra- and interspecific differences in host response times toward alien eggs and cognitive mechanisms involved in host egg discrimination processes. *Key words: Acrocephalus arundinaceus*, brood parasitism, egg discrimination, egg ejection time, great reed warbler, nest inspection. *[Behav Ecol 22:46–51 (2011)]*

Brood parasitism in birds generally imposes considerable costs on host reproductive success (Øien et al. 1998), setting thus in motion the evolution of host counteradaptations. A widespread type of defense adopted by hosts when the other defenses do not prevent the clutch from being parasitized is discrimination against parasitic eggs (Davies 2000).

Egg discrimination is a 2-phase behavioral process consisting of a perception (egg recognition) and an action (egg rejection) component (Hauber and Sherman 2001). Hosts can recognize a parasitic egg by at least 2 cognitive mechanisms (Hauber and Sherman 2001; Moskát and Hauber 2007; Moskát et al. 2010). They may learn the appearance of their eggs and use this information to discard a foreign egg, either by direct comparison (Victoria 1972; Rothstein 1974; Marchetti 2000; Lahti and Lahti 2002) or from memory (Moksnes 1992; Hauber et al. 2006; Moskát and Hauber 2007). The latter method is based on the formation of an inherited memory template of host egg characteristics and on its updating through widening the range of perceived egg traits (Hauber and Sherman 2001; Moskát and Hauber 2007). Assuming that visual perception undoubtedly plays a significant role in this phase of the discrimination process (Langmore et al. 2005), mimicry of parasitic eggs and host intraclutch variation in egg appearance seem to influence host rejection decisions most importantly (Stokke et al. 1999; Cherry and Bennett 2001; Avilés et al. 2006, 2010; Cherry et al. 2007a, 2007b; Honza and Polačiková 2008; Moskát et al. 2008; Underwood and Sealy 2008). Moreover, prospective costs associated with egg rejection and actual risk of parasitism may also affect host motivation to reject (Davies et al. 1996).

By evaluating host responses toward parasitic eggs (sensu Davies 2000), most researchers have dealt only with the action component of egg discrimination. Few authors, however, have considered the perception component of this behavior (see above), for example, through detailed monitoring of hosts immediately after parasitism (Sealy and Neudorf 1995; Soler et al. 2002; Honza et al. 2005, 2007; Antonov et al. 2008, 2009). Apart from a genetic basis (Martín-Gálvez et al. 2006, 2007), egg discrimination has also a conditional component (Øien et al. 1999), which makes it flexible (Lindholm 2000; Lindholm and Thomas 2000) and allows for learning through experience (Hauber et al. 2006; Honza et al. 2007; Moskát and Hauber 2007). In-depth behavioral analyses of experimentally parasitized hosts may therefore contribute to a better understanding of cognitive processes associated with host egg discrimination and may help to explain the individual variability in host behaviors toward parasitic eggs. In this respect, the knowledge of host response times (i.e., how long it takes them to reject an alien egg) may provide an additional insight into their tolerance to foreign eggs.

The duration of time from a stimulus until an appropriate response is an essential characteristic of animal behavior that is required for rational decisions, accurate memory, association of events, and coordination of various behavioral components with each other and with environmental events (MacDonald and Meck 2004). Moreover, as the time needed to make an action can tell us something about the processes by which the information is retrieved (Sternberg 1969), response time procedures are a prominent tool for the study of information processing. To determine the egg rejection times in hosts of brood parasites, their behavior should be monitored

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continuously immediately after parasitism or at least the parasitized clutch should be checked repeatedly at certain intervals. Perhaps because this is often time consuming or even impossible, a lot of studies evaluated host egg rejection times only on a broad scale (in days). Although this method can be informative enough, it does not detect all behavioral displays that could otherwise help to unravel a puzzle why some rejecters delay their egg rejection decisions. The aim of our study was thus 1) an analysis of host behaviors toward a parasitic egg and 2) an assessment of factors potentially influencing host egg rejection times.

METHODS

Model species and experimental procedure

The great reed warbler *Acrocephalus arundinaceus* is an important cuckoo *Cuculus canorus* host (Moskát and Honza 2002; Kleven et al. 2004) with fine-tuned egg recognition abilities (Hauber et al. 2006; Cherry et al. 2007b; Moskát et al. 2008, 2010). The fieldwork was carried out from late April to mid July 2007 in 2 adjacent fishpond areas located between Hodonín (48°51′N, 17°07′E) and Mutěnice (48°54′N, 17°02′E), Czech Republic. In the study period, the local great reed warbler population numbered 60–80 breeding pairs and experienced a relatively high cuckoo parasitism rate (about 36%). Host nests were located in the littoral vegetation, mainly during building or at the beginning of egg laying, and were checked daily to ascertain clutch size, initiation of egg laying, and the incidence of cuckoo parasitism.

Before the start of each experiment, we allowed the birds to habituate to a video setup for 90 min (JVC GZ-MG20E camcorder and tripod; camouflaged in the reeds about 5–10 m from the nest). Afterward, we presented a cuckoo taxidermic mount at focal nests (<1 m from the nest, for 5 min or till the contact attack), and after its removal, we parasitized host clutches with a nonmimetic egg. We used mainly great reed warbler eggs ($n = 31$); in the remainder of tests, we used eggs from abandoned song thrush *Turdus philomelos* ($n = 11$) and red-backed shrike *Lanius collurio* ($n = 2$) nests. We either added an egg to the host clutch (in cases when ≤ 3 eggs were present, $n = 18$) or swapped it with 1 randomly chosen host egg (when ≥ 4 eggs were present, $n = 26$), so that the total number of eggs in the tested nests did not differ between these 2 groups (median for both addition and exchange = 5; Mann–Whitney test, $U = 179.5$, $P = 0.19$, $n_1 = 18$, $n_2 = 26$). All experimental eggs had been painted with acrylic blue (Pantone color code: 299 C) before they were inserted into host nests. The nests were experimentally parasitized within 4 days after the laying of the penultimate egg, between 8:00 and 11:00 h Central European Time.

Immediately after clutch manipulation, we video recorded host behavior continuously within the same day until dusk (without disturbance of nest owners). If hosts did not reject the egg during this period, we removed the video setup and visited the nest on the following day (and then daily) to obtain at least a rough estimate of the rejection time. If the egg remained in the host nest for 5 days, it was considered accepted. Only nests with precisely known egg ejection times ($n = 30$) were included in further analyses. To avoid pseudoreplications, we color-banded individual birds and tested them only once.

Variables subjected to analyses

The response variable, timing of egg ejection, was extracted from video recordings as the time elapsed from the first arrival of the female on the nest to ejection of the experimental egg. As in the great reed warbler, the female is solely responsible for egg ejection (Požgayová et al. 2009); we took into account only female-related characteristics as explanatory variables (clutch inspection behavior and body condition) and eggshell coloration characteristics (intraclutch variation in blue-green chroma and mean clutch brightness). As explanatory variables, we also considered egg-laying date, egg volume differences between foreign and host eggs, and the incidence of natural parasitism.

The time the female spent by clutch inspection was extracted from video recordings and was expressed relatively to the total time she spent on nest. Clutch inspection (sensu Moksnes et al. 1993) covered all activities during which the females had a visual contact with their eggs, such as egg turning or observing the clutch, i.e., when they were standing in the nest (or on its rim) either watching the eggs or pecking down into the nest.

Female condition was calculated as residuals from regression of body weight on tarsus length. Eggshell coloration was measured using a USB2000 spectrophotometer (Ocean Optics; for detailed methods see Polačiková et al. 2009). Great reed warblers lay eggs of pale green, blue, or blue-green background color, speckled and blotched olive-green, pale blue-gray, and dark brown (Cramp 1992) and the reflectance curve of the eggshells corresponds to their general blue-green appearance to the human eye. As blue-green chroma has been shown to serve as signal of female quality (Moreno and Osorno 2003; Polačiková et al. 2009) and intraclutch variation influences host egg discrimination (Stokke et al. 1999; Cherry et al. 2007b; Moskát et al. 2008), we used intraclutch variation in blue-green chroma. This color characteristics was calculated for each clutch as a standard deviation in blue-green chroma (Dale 2006), which we expressed as the ratio of reflectance in the blue-green part of the spectrum to the total reflectance ($R_{400-575}/R_{325-700}$; Cassey et al. 2008). In addition, we used the mean clutch brightness (i.e., the sum of the total reflectance values within the 325–700 nm range of wavelengths, averaged per clutch) as a measure of achromatic variance.

As egg-laying date, we took the day when the first egg of a clutch appeared in a nest (1 May = day 1). The length (L) and breadth (B) of host and experimental eggs were also measured to calculate egg volume (V) according to Hoyt (1979): $V = 0.51 \times L \times B^2$. To take into account the size variation of experimental eggs, we subtracted mean host egg volume from the volume of a foreign egg.

Some of the nests (16/44) were naturally parasitized by the cuckoo before the start of the experiment. However, once detected, cuckoo eggs were collected for purposes of another study. As the presence of a parasitic egg could put hosts on alert and accelerate their subsequent behavior, a binary variable (0 = not parasitized and 1 = parasitized) was also included into analyses.

Statistical analyses

As the dependent variable (timing of egg ejection) was not normally distributed (Figure 1) and could not be properly transformed, we carried out a regression tree analysis—a nonparametric counterpart to traditional linear techniques (Breiman et al. 1984). Regression trees are not subject to any strict assumptions: the data need not be normally distributed, the results are not influenced by outliers, explanatory variables may be continuous or categorical, even intercorrelated, and there is no assumed linearity between independent and dependent variables.

The regression tree analysis is based on recursive binary splitting of the original data. Each split is made by considering every available predictor (in turn) as a potential splitting variable. At each split point (node), such value of the splitting variable is chosen that yields the maximum difference between the values of the dependent variable in the 2 resulting subsets.

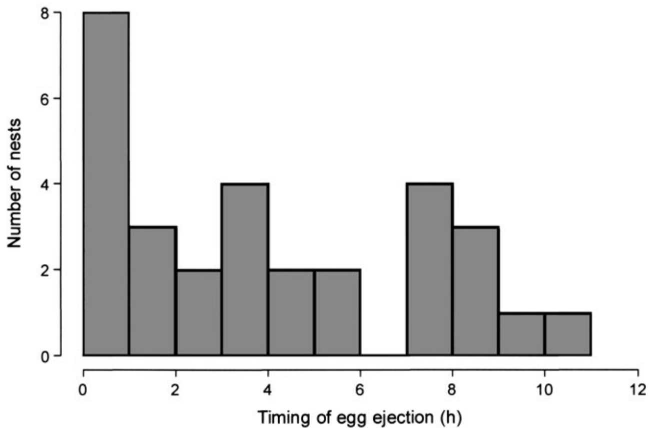


Figure 1
Timing of egg ejection in the great reed warbler, as revealed by video recording ($n = 30$).

This procedure enables the development of a tree with a root (undivided data; at the top), branches, and leaves (terminal nodes). The terminal nodes have values of the dependent variable, which are predicted under chains of given conditions. These values are the averages of the observed response variables. The measure used to build the model is the averaged sum of squares, averaged over all terminal nodes. The predictor variable and splitting value that resulted in the greater reduction in the averaged sum of squares are selected. Unlike stepwise regression, all predictors and all possible splitting values of each prediction variable are evaluated at each split independently, which allows detecting complex interactions among explanatory variables (Karels et al. 2004). This statistical method has increasingly found applications both in behavioral (Grubb and King 1991; Fuiman et al. 2006; Low et al. 2006) and ecological studies (Rejwan et al. 1999; O'Connor and Wagner 2004).

We first allowed the regression tree to grow to its maximum size and then pruned it back to the optimal size to verify its prediction accuracy. This process is necessary, as a large tree that is overfitted to the certain data set is very good at predicting the data used to build the model, but poorly predictive of any new data (De'Ath and Fabricius 2000). To determine the optimal tree size, we used a leave-one-out cross-validation algorithm and chose the model that best predicted the excluded data. To carry out regression tree analyses, we used rpart library implemented in R (R Development Core Team 2009).

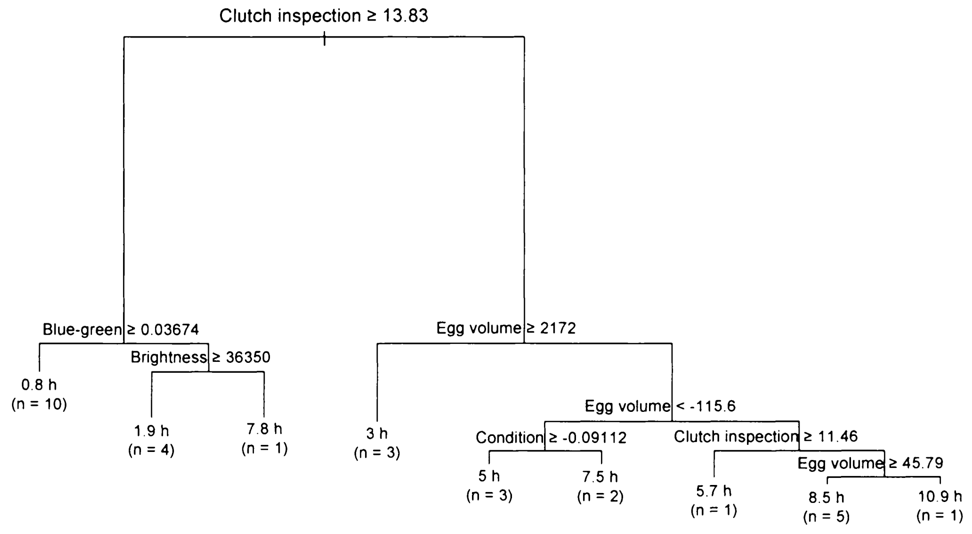
RESULTS

From the total of 44 experiments, the nonmimetic egg was rejected in 40 (91%) cases; in the remaining 4 (9%), it was accepted. The vast majority of eggs (35/40) were rejected within 1 day from egg insertion, 4 within 2 days, and 1 within 3 days. The method of rejection was puncture ejection, but in 4 cases, the host clutch was subsequently also deserted. By continuous video recording, we documented 30 egg ejection events (all within 1 day from the start of the experiment). The time it took the hosts to eject the foreign egg was highly variable (Figure 1; median = 3.2 h, lower quartile = 0.9 h, upper quartile = 7.7 h, $n = 30$). In 8 (27%) events, the egg was ejected very quickly (within 1 h).

We fitted the regression tree model with a suite of female-related characteristics (size-corrected mass, intraclutch variation in eggshell blue-green chroma, laying date, mean clutch brightness, and % of time spent by clutch inspection), difference between host and experimental egg volume and occurrence of natural cuckoo parasitism as predictors, and timing of egg ejection as the dependent variable. The full initial regression model (Figure 2) showed that females, who spent more than 14% of the time by clutch inspection, ejected the foreign egg more quickly than females inspecting the clutch less than 14% of the time. The proportion of time the females spent by clutch inspection explained most of the variability in the initial model ($R^2 = 0.558$; shown also by the length of branches).

Cross-validation showed that only the proportion of time the females spent by clutch inspection reliably predicted the

Figure 2
Full regression tree model of factors possibly affecting the timing of egg ejection in the great reed warbler. The tree is constructed according to a series of splitting criteria. If the condition in the node is fulfilled, proceed to the left. Averaged ejection times, together with n are given in terminal nodes. The length of branches shows the proportion of explained variability. Explanatory variables selected by the model: % of time spent by clutch inspection (clutch inspection), intraclutch variation in blue-green chroma (blue-green), mean clutch brightness (brightness), volume difference between host and experimental egg (egg volume), and residuals from regression of body weight on tarsus length (condition).



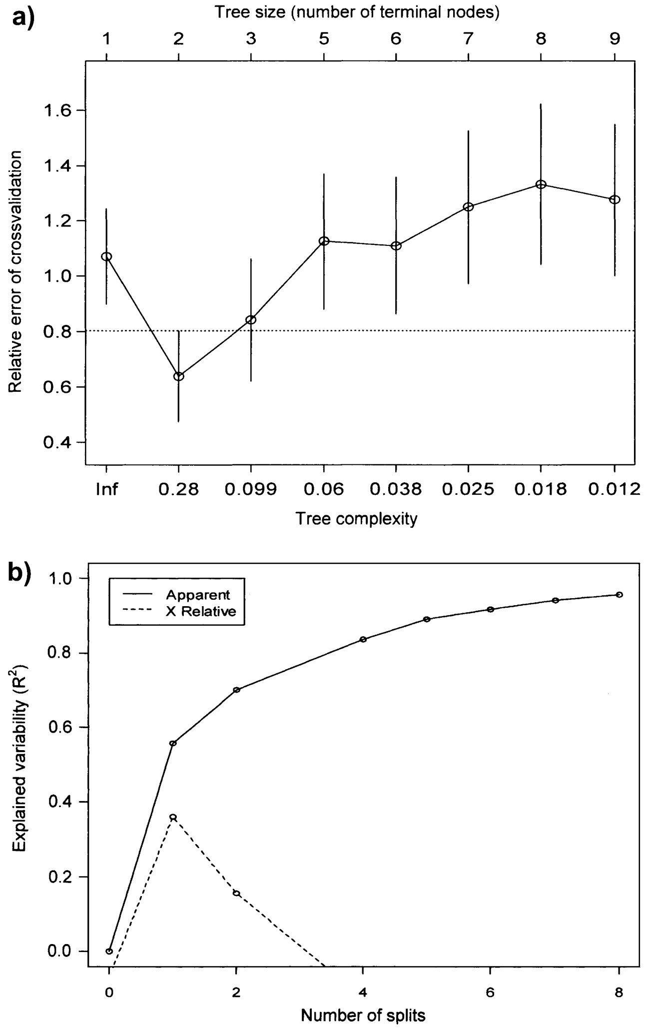


Figure 3
Prediction accuracy of regression trees obtained by cross-validation. (a) Mean relative error estimated by cross-validation. The most accurate and most parsimonious model is that with only 2 terminal nodes (i.e., 1 split). (b) Comparison of apparent and relative variability explained by the full (apparent) and cross-validated (X relative) model, respectively. The tree with only 2 branches explained the most of the variability.

timing of egg ejection. The mean relative error estimated by cross-validation decreased rapidly to the tree with only 2 branches and then increased again with growing tree size (Figure 3a). Pruning the tree back to this size (i.e., 1 split with 2 branches), we obtained the most parsimonious tree with the best prediction accuracy (Figure 3b).

DISCUSSION

Timing of egg rejection

Besides rejection rates, the information on rejection times extends our understanding of behavioral plasticity in host responses toward parasitic eggs. However, due to general scarcity of studies referring to the timing of host egg rejection, there are only a couple of instances allowing a meaningful comparison. In the present study, the vast majority (88%) of great reed warblers ejected a foreign egg within the same day when it was inserted into the nest (see also Antonov et al. 2008 for similar findings in the marsh warbler *Acrocephalus palustris*). However, in the blackcap *Sylvia atricapilla*, 38% of the tested pairs delayed their response until the second day (Honza M, Požgayová M, and Procházka P, unpublished data). The highest proportion of great reed warblers ejected the foreign egg within an hour from its insertion (8/30; Figure 1), whereas blackcaps did not eject until 2.3 h and the highest proportion of ejected eggs fell between 4 and 5 h after egg insertion (6/19, own unpublished data). Extremely quick ejection of a foreign egg (within minutes or even seconds) was found in northern orioles *Icterus galbula* (Sealy and Neudorf 1995) and some thrushes *Turdus* spp. (Honza et al. 2005; Samaš P, Hauber ME, Cassey P, and Grim T, in preparation). On the other hand, most cedar waxwings *Bombycilla cedrorum* takes several days to reject an alien egg (Rothstein 1976). Although not numerous, these and other studies (e.g., Moksnes et al. 1993; Soler et al. 2002; Honza et al. 2007) documented that there is a high variation in the timing of egg rejection both within and among host species, with some rejecters responding very quickly, whereas others lagging behind.

Factors affecting host rejection times

Our results indicate that the proportion of time the hosts devoted to clutch inspection played a major role in shaping their responses toward a foreign egg. More specifically, great reed warbler females that inspected their parasitized clutches more and ejected the introduced egg more quickly than females that were little engaged in clutch inspection. These findings are in accordance with suggested cognitive mechanisms most probably adopted by hosts recognizing parasitic eggs (Hauber and Sherman 2001; Moskát and Hauber 2007; Moskát et al. 2010). As these hosts are assumed to be mainly responsive to visual stimuli from their clutches (Langmore et al. 2005), they need an appropriate amount of time to process the visual cues on the eggshells. Although egg pecking has been used as an indication of egg recognition (Antonov et al. 2008, 2009), more attention should be paid also to clutch inspection, during which egg recognition processes take place. Another nice example highlighting the significance of nest inspection behavior comes from a study of Johnson et al. (2008), who found that nest inspection is necessary to induce a transition to nestling provisioning in male house wrens *Troglodytes aedon.*

Apart from the clutch inspection behavior, host perceptual abilities may also contribute to the explanation of the differences in rejection times. Indeed, several studies found that it took hosts longer to reject mimetic compared with nonmimetic eggs (Lotem et al. 1995; Honza et al. 2004, Antonov et al. 2008, but see Procházka and Honza 2003, 2004). Rejection of a nonmimetic egg may be a straightforward and error-proof task, allowing relatively quick responses, which may also apply to our results. On the contrary, to reduce the risk of errors, mimetic eggs require a prolonged period of recognition until rejection could be released (Davies et al. 1996; Rodríguez-Gironés and Lotem 1999; Stokke et al. 2005). Additionally, intraclutch variation in host egg appearance may also influence host responses, with higher variation hindering egg recognition (Stokke et al. 1999; Moskát et al. 2008, but see e.g., Cherry et al. 2007b for the opposite). Yet, Lotem et al. (1995) and Karcza et al. (2003) did not find any association between the intraclutch variation and host egg rejection rates. Similarly, we found no effect of intraclutch variation in egg appearance on timing of host responses toward a parasitic egg.

Shell thickness and strength of the parasitic egg (real or artificial) may also influence host reaction times (Antonov et al. 2008, but see Honza and Moskát 2008). In this context, puncture ejectors need more time to break the egg and eat some of its contents, whereas grasp ejectors eject quickly, picking up the egg with their mandibles. Marsh warblers in the study of Antonov et al. (2008) ejected the nonmimetic real cuckoo eggs significantly later than identically painted great reed warbler eggs, which was attributable to a greater pecking effort needed to puncture hard-shelled cuckoo eggs. In our study, we used experimental eggs with comparable shell thickness, but of different size (see METHODS); however, the volume of the experimental egg had no effect on host response times. We suggest that due to body size differences, larger puncture ejectors (like great reed warblers) may experience fewer difficulties with egg ejection than smaller puncture ejectors (like marsh warblers or blackcaps), irrespective of egg type used.

Response times toward foreign eggs may differ between pair members, as well; with 1 sex being a quicker ejector than the other. In accordance with this, Honza et al. (2007) found that in the blackcap, where both parents show egg discrimination abilities, females ejected a foreign egg significantly more quickly than males. Similar intersexual differences in timing of egg ejection were documented in northern orioles, where males incur also more ejection costs (Sealy and Neudorf 1995). Perhaps, a lack of experience with the parasitic egg causes males to be less apt egg rejecters than females. The importance of previous experience on host egg rejection times has been tested by Honza et al. (2007). By parasitizing and video recording host pairs in 2 consecutive trials within 1 breeding attempt, they found that the response time in the second trial was significantly shortened in comparison to the first trial. Moreover, rejection in the second trial was faster if the ejector was the same individual, which suggests that there is a learning component involved in egg rejection behavior. Perhaps, the high proportion of quick ejectors in the present study was caused by testing individuals already experienced with brood parasitism. This may be truth, bearing in mind that our great reed warbler population is under a relatively high parasitic pressure from the side of the cuckoo (approximately 36% in 2007), and the interannual breeding site fidelity is high in adults (61% of 80 adult females ringed or controlled in 2007 returned to our study site in 2008).

By continuous video recording of hosts after experimental parasitism, we demonstrated for the first time that clutch inspection is of importance when hosts are discriminating against foreign eggs because during this behavior, egg recognition is most probably set in motion. Accordingly, we suppose the following sequence in which egg ejection process could proceed from looking into the nest, through egg turning toward soft pecking, and, eventually, more vigorous pecks (sensu Antonov et al. 2008). In this study, we further discovered that individual differences in clutch inspection behavior may explain a substantial proportion of variation in host egg ejection times. We encourage researchers to assess the proximate mechanisms of egg recognition and rejection by exploring the behavior of parasitized hosts.

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