

1 **How to spot a stranger's egg? A mimicry-specific**  
2 **discordancy effect in the recognition of parasitic eggs**

3

4 **Csaba Moskát<sup>1</sup>, Anikó Zölei<sup>2</sup>, Miklós Bán<sup>3</sup>, Zoltán Elek<sup>1</sup>, Lainga Tong<sup>4</sup>,**  
5 **Nikoletta Geltsch<sup>5</sup> and Márk E. Hauber<sup>4</sup>**

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7

8 <sup>1</sup> MTA-ELTE-MTM Ecology Research Group, Biological Institute, Eötvös Lóránd  
9 University, Pázmány Péter sétány 1/C., H-1117 Budapest, Hungary and Hungarian Natural  
10 History Museum, Baross u. 13., H-1088, Hungary

11 <sup>2</sup> Department of Systematic Zoology and Ecology, Eötvös Loránd University, Pázmány Péter  
12 sétány 1/C, H-1117 Budapest, Hungary

13 <sup>3</sup> MTA-DE "Lendület" Behavioural Ecology Research Group, Department of Evolutionary  
14 Zoology, University of Debrecen, Egyetem tér 1, H-3010 Debrecen, Hungary

15 <sup>4</sup> Department of Psychology, Hunter College and The Graduate Center of the City University  
16 of New York, NY 10065, USA

17 <sup>5</sup> Department of Ecology, University of Szeged, Közép fasor 52, Szeged, H-6726, Hungary

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25 **Abstract**

26

27 Egg discrimination by hosts is an antiparasitic defence to reject foreign eggs from the nest.

28 Even when mimetic, the presence of brood parasitic egg(s) typically alters the overall

29 similarity of all eggs in a clutch, producing a discordant clutch compared to more

30 homogenous clutches of composed only of hosts' own eggs. In multiple parasitism, the more

31 foreign eggs are laid in the nest, the more heterogeneous the overall clutch appears.

32 Perceptual filters and recognition templates cannot explain the known pattern of lower

33 rejection rates of foreign eggs in multiple vs. single parasitism. We therefore assessed the role

34 of clutch homogeneity and manipulated the colour of one or more eggs in the clutches of great

35 reed warbler (*Acrocephalus arundinaceus*) hosts of common cuckoos (*Cuculus canorus*).

36 Varying the colours of both the majority and the minority eggs caused predictable shifts in the

37 rejection of the focal egg(s), and ejection rates of the minority egg colour consistently

38 increased but only when it belonged to a more mimetic egg colour, relative to the less

39 mimetic colour of majority eggs. The results imply that in addition to sensory filters, and

40 template-based cognitive decision rules, discordancy-based rejection is affected by the overall

41 clutch appearance, and interacts with specific colours varying in the extent of mimicry, to

42 contribute to the recognition decisions of hosts to reject parasitic eggs.

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45 Keywords: brood parasitism, cuckoo, great reed warbler, egg discrimination, clutch

46 characteristics, discordancy

47

48 Short title: Clutch variation and egg discrimination

## 49 **Introduction**

50

51 Rejecting a foreign egg in the nest is one of most effective steps in eliminating interspecific  
52 avian brood parasitism by hosts (Davies 2011). However, egg discrimination is a rather  
53 general phenomenon, not restricted to cases of interspecific brood parasitism, as similar  
54 mechanisms also occur in intraspecific parasitism (e.g. Yom-Tov 1980; Lyon 2007; Hoi et al.  
55 2010). Egg discrimination is a complex cognitive task (de la Colina et al. 2012), especially in  
56 the face of egg colour and pattern mimicry of the hosts' own eggs by the parasites (Stoddard  
57 and Stevens 2010; 2011), and only some host species and certain individuals do so with  
58 consistent success (Samaš et al. 2011).

59 Hosts may recognize a foreign egg based on differences in its appearance from the rest  
60 of the eggs in the clutch, through the rule of discordancy (Rothstein 1975, Sealy &  
61 Underwood 2012), so that eggs in the majority are regarded as own eggs, to be accepted,  
62 whereas egg(s) in the minority are regarded as parasitic, to be eliminated (Stokke et al. 1999;  
63 Moskát et al. 2008a). Alternatively, hosts may have a perceptual filter or a recognition  
64 template, coupled with a discrimination threshold, for own eggs (Rothstein 1975; Lyon 2007;  
65 Petrie et al. 2009), so that they do not rely on inspecting own eggs during discrimination to  
66 make rejection decisions (Hauber & Sherman 2001; Bán et al. 2013). However, even rejecters  
67 might experience perceptual and cognitive constraints limiting the success of egg recognition  
68 (Krüger 2011), depending on intrinsic factors (age: Lotem et al. 1995; clutch inspection  
69 behaviour: Požgayová et al. 2011; Polačiková et al. 2013), or extrinsic factors (e.g., variation  
70 in the extent of host-parasite mimicry: Cherry et al. 2007a; ambient light conditions: Honza et  
71 al. 2011; or the number of parasitic eggs in the nest: Stevens et al. 2013).

72 Both discordancy and threshold-based recognition mechanisms are efficient because  
73 eggs laid by the same female bird (the host) typically show greater similarity to each other  
74 compared to eggs laid by different females, including brood parasites (Stokke et al. 2007;  
75 Cassey et al. 2011; Honza et al. 2012). Accordingly, even in brood parasitism with mimetic  
76 eggs, the foreign egg is typically more dissimilar from the others, disrupting the visual  
77 homogeneity of the clutch (Stokke et al. 1999; Moskát et al. 2008a ). Thus, in most hosts,  
78 resulting in discordant clutches in parasitized nests (Moskát et al. 2010; Stevens et al. 2013).

79 Here we evaluated whether and how in great reed warblers (*Acrocephalus*  
80 *arundinaceus*), a host locally heavily impacted by single or multiple parasitism of the  
81 common cuckoo (*Cuculus canorus*) (Moskát et al. 2009), egg discrimination behaviours are  
82 altered by characteristics of the whole clutch, depending on the relative proportions of

83 differently mimetic egg colours in the clutch. Based on past research (Bán et al. 2013), we  
84 hypothesized that if a clutch contains at least two different egg phenotypes, it is the extent of  
85 each phenotypes difference in egg appearance from the hosts' own eggs, and not their relative  
86 status (i.e. majority or minority eggs), that determines the likelihood of egg rejection.

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88

## 89 **Material and Methods**

90

### 91 *Study site and species*

92

93 The study was conducted in the surroundings of Apaj (47°07'N; 19°06'E), ~50 km south of  
94 Budapest, Hungary, where common cuckoos commonly parasitize great reed warblers  
95 (Moskát & Honza 2002). We searched for nests of hosts in 2-4 m wide reed beds of small  
96 channels between May 15 and June 15, in 2009, 2011 and 2013 (for more details on the field  
97 work, see Moskát and Hauber 2007). Pseudoreplication of our unbanded subjects, within and  
98 across years, was likely low because we did not use nests in the same territory repeatedly and  
99 because breeding philopatry is known in this population (Moskát et al. 2008b).

100

### 101 *Experimental treatments and controls*

102

103 Observations of cases of natural parasitisms by cuckoos, involving typically just one parasitic  
104 egg and several host eggs in a clutch, do not permit researchers to explore the underlying  
105 mechanism of egg discrimination in hosts of brood parasites. This task needs focal  
106 experiments, where the proportion of parasitic eggs in a clutch, as well as the appearance of  
107 the parasitic eggs, are manipulated (Moskát & Hauber 2007; Moskát et al. 2010). As the  
108 shape of the egg in a clutch may affect egg recognition and rejection decisions in the great  
109 reed warbler (Bán et al. 2011; Zölei et al. 2012), we simulated brood parasitism by painting  
110 (dyeing) hosts' own eggs with highlighter pens, generating foreign eggs which resemble host  
111 eggs in size, shape, and maculation pattern, but differ in background colour (Bán et al. 2013).  
112 We manipulated eggs on the day when the clutch was predicted to reach the modal clutch size  
113 of five eggs in this population (e.g. Moskát et al. 2011). As these warblers lay one egg per day  
114 (Leisler & Schulze-Hagen 2011), this was the fourth day following the appearance of the first  
115 host egg in a clutch. In order to generate a representative sample of egg discrimination  
116 decisions in our great reed warbler population, we also used nests for experiments with four

117 and six eggs (4 eggs: 10 clutches, 5 eggs: 111 clutches, 6 eggs: 6 clutches). When hosts laid  
118 an extra (6th) egg, it was left unmanipulated or painted with the colour of the majority egg  
119 type in experiment (see below).

120 Altogether, we applied one of six treatments to 95 nests (Fig. 1a):

121 "1 green and 4 natural eggs" treatment: One egg in clutch was painted green, and all other  
122 eggs in clutch remained natural (unmanipulated).

123 "1 green and 4 blue eggs" treatment: One egg was painted green and the rest were painted  
124 blue.

125 "1 green and 4 orange eggs" treatment: One egg was painted green and the rest were painted  
126 orange

127 "1 orange and 4 natural eggs" treatment: One egg in clutch was painted orange, and the other  
128 eggs remained natural.

129 "1 orange and 4 blue eggs" treatment: One egg was painted orange and the rest were painted  
130 blue.

131 "1 orange and 4 green eggs" treatment: One egg was painted orange and the rest were painted  
132 green.

133 We used Stabilo Boss, non-toxic highlighter pens for dying, types 70/33 (green) and  
134 70/54 (orange). We compared nests with natural eggs and a dyed ('parasitic') egg (green or  
135 orange) with treatments of the same parasitic egg accompanied with parasitic eggs of the  
136 other colour (green-orange and orange-green egg types in the minority and majority of the  
137 clutches). We chose these egg types as differently mimetic artificial egg colours, based on the  
138 calculated avian perceptual model of these eggs against natural eggs (see below), and on the  
139 previously known patterns that great reed warblers respond to green vs. orange dyed eggs  
140 differently (14% vs. 77% rejection rates toward the green and the orange eggs, respectively, in  
141 single parasitism, Bán et al. 2013).

142 As host individuals had the chance to learn the appearance of each of their own,  
143 unmanipulated eggs before our experiments started, i.e. during egg laying, we used the  
144 treatments with light blue eggs (Stabilo Boss 70/31; treatments "1 green and 4 blue eggs" and  
145 "1 orange and 4 blue eggs") to control for this potential learning effect in the "1 green and 4  
146 natural eggs" and "1 orange and 4 natural eggs" treatments. . We chose this egg type as  
147 previously we reported the lowest rejection rate toward this among differently dyed host own  
148 eggs (7% rejection rate in single parasitism, Bán et al. 2013). This means that hosts had four  
149 days to view and learn about their natural eggs before the experiment with dyed eggs started  
150 on the fifth day after the onset of laying (5d). We dyed eggs blue on 5d, to parallel the

151 experimental methods for all dyed egg colours, so that all subjects are not exposed to the  
152 manipulated egg colours until the same day of the laying cycle, across the different  
153 treatments.

154 As unmanipulated controls, we monitored with the same frequency several non-  
155 parasitized clutches in the same years at our study population, and no desertions or egg losses  
156 were observed in any of them ( $n = 21$ ).

157 The treatment to dye eggs did not cause any failure on host reproduction. We tabulated  
158 the results our experiments when the nest was monitored at least until hatching, including  
159 results of a previous study when different colours of Stabilo Boss highlighter pens were  
160 applied (blue, green, yellow, red and orange; Bán et al. 2013 and the present study). Egg  
161 hatching rates (%) per clutch did not differ between control nests (mean =  $91.24 \pm 2.188$  SE)  
162 and experimental nests (mean =  $91.32 \pm 2.314$  SE) where one or more eggs were dyed (Mann-  
163 Whitney  $U_{41,22} = 429$ ,  $P = 0.708$ ).

164 Nests were monitored daily for six consecutive days after treatment (e.g. Moksnes et  
165 al. 1991; Moskát et al. 2009). If an egg remained in the nest after the monitoring period, the  
166 result was regarded as acceptance; missing eggs were regarded as ejected. Only one nest was  
167 deserted (in the "1 green and 4 natural eggs" treatment) and we omitted it from the analyses.  
168 In one nest of the "1 green and 4 blue eggs" treatment, the green parasitic egg was not ejected  
169 on the first day of monitoring, but all of the accompanying four blue eggs were removed, and  
170 then the nest with the remaining single green egg was deserted. We categorized it as post-  
171 ejection nest desertion (sensu Moskát et al. 2011), where desertion was probably caused by  
172 the reduced clutch size. As "post ejection nest desertion" was a quick response here (observed  
173 after one day the experiment started), reducing potential response period of host from six days  
174 to only one, we omitted this nest from the data set used for statistical analyses of single  
175 (green) parasitic eggs. However, we could use the ejection of the blue eggs as response to the  
176 majority egg type.

177

### 178 *Visual modelling of egg types*

179

180 Representative reflectance spectra of natural and experimental eggs were measured by Ocean  
181 Optics USB 2000 spectrometer and taken from Bán et al. 2013 (with the averages shown in  
182 Fig. 1b). Reflectance data were tabulated for the avian perceivable 300-700 nm range at 3  
183 different points/egg. We carried out avian visual modelling and calculated just noticeable  
184 chromatic differences (JNDs) between randomly chosen pairs of host natural and dyed egg

185 colours, with the program Avicol 6.0 (Gomez 2006), following parameters and specifications  
186 of Igic et al. (2012), based on a broken canopy nest light environment and an ultraviolet  
187 sensitive oscine, the European blackbird (*Turdus merula*) (Aidala et al. 2012). Although the  
188 absolute values of JNDs from perceptual modelling depend on the parameterization of the  
189 particular sensory model (Igic et al. 2010), their relative values could be informative about the  
190 extent of visual mimicry regarding how hosts' perceptual system can recognize and  
191 distinguish foreign egg colors from own eggs (Avilés 2008; Spottiswoode & Stevens 2010).

192

### 193 *Statistical analyses*

194

195 Generalized linear models were used to analyse the relationship between the assumed  
196 explanatory variables and the ejection event of the single eggs as a binary response variable  
197 (where 0 denotes the acceptance, and 1 is for rejection) and the number of eggs ejected (as  
198 count data). Two classes of null distribution were used: "binomial" for occurrence data and  
199 "Poisson" for count data. For selecting the most parsimonious model, we applied the above  
200 mentioned multi-model inference. The differences between the levels of the tested factor  
201 (treatment) were evaluated by multiple comparisons (with Tukey computed contrast matrices  
202 for several multiple comparison procedures). The goodness of the models' fit (compared to the  
203 null model) was tested by a likelihood ratio test. The analyses were carried out in R 3.0.1 (R  
204 Core Team 2013), using the package MuMIn for multi-model inference (Barton 2013),  
205 package multcomp (Hothorn et al. 2008) for multiple comparisons and the package lrttest for  
206 likelihood tests (Zeileis & Hothorn 2002).

207 The model parameters were investigated by multi-model inference (Burnham and  
208 Anderson 2002) in order to explore the effect of the explanatory variables such as treatment,  
209 year, clutch size, number of days until the first egg laying and the latency in the egg rejection  
210 on the response variables such as occurrences of ejection (binary) and the number of eggs  
211 ejected (count). This approach was applied on the dataset for the rejection rate of the minority  
212 egg type, and the dataset of the majority egg type. For each explanatory variable, we used an  
213 information criterion (AICc) to rank the single-argument models in terms of their ability to  
214 explain the frequency of ejection or number of eggs ejected (Burnham & Anderson 2002;  
215 STable 1). In this way, a "best approximating" model of parameters was selected for the most  
216 parsimonious explanation of the data. In the case of both dataset (minority and majority) the  
217 latency were excluded from further analyses due to high number of missing values which  
218 might distort the model fit. The clutch size was added as a correction term for dispersion

219 parameter (Bolker et al. 2009) to control for the potential effect of different clutch sizes on the  
220 response variables (Moskát et al. 2011). For the dataset of the majority egg type, the year was  
221 not considered as previous studies on this population did not reveal any year effect (e.g.  
222 Moskát & Hauber 2007, Moskát et al. 2009, 2010; for details see STable 1 in the Supporting  
223 Material).

224

225

## 226 **Results**

227

### 228 *Visual modelling of egg types*

229

230 Perceptual modelling revealed that dyeing host eggs with the three different colours generated  
231 a significant variation in the extent of perceivable differences from the hosts' own eggs ( $F_{8,24}$   
232 = 8.0,  $P = 0.007$ ). Plotting the JND values against those generated by comparisons of host  
233 eggs against other conspecifics, revealed that blue eggs were most similar, green eggs  
234 intermediate, and orange eggs least similar to the host eggs (Fig. 1c).

235

### 236 *Ejection rates toward the experimental eggs*

237

238 Great reed warblers showed a broad range of variation in ejection rates toward the minority  
239 egg type in response to the different treatments (11-75%; Fig. 2a). We detected 25-56%  
240 ejection rates (ejection/clutch) when the two experimental egg types (green or orange) were in  
241 the majority in the clutch. Ejection rates toward the two other egg types (natural and blue) in  
242 the majority of the clutch were 0-7% (Fig. 2b). Consequently, we observed high numbers of  
243 multiple egg ejections from clutches containing both green and orange eggs. In the "1 green  
244 and 4 orange eggs" treatment, i.e. when a green egg was accompanied with four orange eggs,  
245 93.3% of all eggs were ejected from nests where ejection occurred ( $n = 9$ ). In the "1 orange  
246 and 4 green eggs" treatment 47.8% of all eggs were ejected from nests where ejection took  
247 place.

248

249

### 250 *Approximation of the most parsimonious model*

251



252 For the dataset on the minority eggs we tested two candidate models (see STable 2) and we  
253 found that the frequency of rejection and the number of eggs rejected were best described by  
254 the models where the treatment and the laying date were included as explanatory variables.  
255 For the majority eggs, we also tested two models, and we found that the reduced model was  
256 the most parsimonious one for both response types (STable 2).

257

258 *Estimating discordance by the most parsimonious models*

259

260 In the cases of the different minority egg colours, there was significant difference among the  
261 treatments, but laying date had no effect on the frequencies of ejections (Table 1). The  
262 multiple model comparisons revealed that most of the differently mimetic colour  
263 combinations ("1 green and 4 natural eggs" vs. "1 orange and 4 natural eggs" or "1 green and  
264 4 blue eggs" vs. "1 orange and 4 blue eggs" treatments") resulted in significantly different  
265 rejection rates (Table 2). However we detected no statistical differences in the numbers of  
266 eggs rejected neither between the treatments nor for laying date (Tables 1 and 2; 95%  
267 confidence intervals are shown in STable 3).

268 For the majority egg types, the likelihood test revealed that the binary model was not  
269 significantly different from the null model (STable 4), thus the estimates from this model are  
270 not reported here. The model for the number of eggs ejected revealed significant differences  
271 among the treatments (Table 1), so that combinations of differently mimetic egg colours  
272 improved the ability of birds to recognize differently-coloured parasitic eggs (Table 2).

273

274

## 275 **Discussion**

276

277 Exploring the sensory and cognitive mechanism of how hosts of brood parasites discriminate  
278 among own vs. foreign eggs in their clutches is at the core of testing coevolutionary arms  
279 races between host defences in recognition systems and parasitic counteradaptations of egg  
280 phenotypes, and it has been a great challenge for researchers because most experiments rely  
281 on egg rejection behaviour to detect perceptual discrimination (Davies 2000; Rothstein &  
282 Robinson 1998; but see Antonov et al. 2009; Požgayová et al. 2011; Moskát et al. 2014).  
283 Recent studies have confirmed the most prevalent prediction for the evolution of parasitic egg  
284 colour and pattern mimicry, initially tested by human observers (Davies 2000), that less

285 mimetic eggs, when seen by the avian eye, are rejected more often (Cassey et al. 2008; Avilés  
286 et al. 2010; Spottiswoode and Stevens 2010; Croston & Hauber 2014; Stevens et al. 2013).

287 In our study, we focused on the perceptual mechanisms of egg recognition, which is  
288 the first step in the egg discrimination process (Soler et al. 2012). Previous results on the great  
289 reed warbler, a frequently parasitized host species of the common cuckoo, already revealed  
290 that these birds primarily use template-based egg recognition mechanism in order to recognize  
291 the parasitic egg(s) in clutch, so they can discriminate the parasitic eggs even when there is no  
292 own egg in the clutch (Moskát & Hauber 2007; Moskát et al. 2010; Bán et al. 2013).

293 However, in addition to template recognition, these hosts can also rely on discordancy, as  
294 when they recognize and reject the egg phenotype presenting in the minority of the clutch  
295 (Moskát et al. 2010). However, discordancy is error prone, especially in multiple parasitism,  
296 as it might lead to the ejection of single own eggs if they are accompanied by several parasitic  
297 eggs, as may be possible nests with multiple parasitisms (Rothstein 1974; Moskát et al. 2010).

298 The present study revealed a new aspect of egg recognition, and a complexity of the  
299 discordancy-based rejection mechanism, by demonstrating that the majority egg type's  
300 coloration, especially when it differs in mimetic appearance from hosts' own eggs, affects the  
301 rejection of the minority egg types in discordant clutches. This result suggests that  
302 discordancy is a contributing and interactive process with other decision rules involved in egg  
303 recognition, and not necessarily a stand-alone mechanism as previously thought by some  
304 (reviewed by Moskát et al. 2010). Our new data set up the need for further research to reveal  
305 the presence of the role of discordancy in egg recognition in other species that discriminate  
306 and reject the parasitic egg. In addition, discordancy-based mechanisms may also have  
307 relevance for cognitive processes in intraspecific brood parasitism, where the parasitic  
308 (conspecific) eggs are typically a close match ("mimetic") of the host's own eggs, yet several  
309 hosts respond to intraspecific parasitism by ejecting foreign eggs, burying the foreign eggs, or  
310 deserting the parasitized clutches, (Davies 2000); with sometimes many of them rejected from  
311 a clutch (e.g. up to six parasitic eggs in the bearded tit, *Panurus biarmicus*; Hoi et al. 2010).  
312 Variation in the colour, size and shape of eggs, or in general, foreign objects in the nest, may  
313 motivate ejections in conspecific parasitism (Poláček et al. 2013), similarly to cases in  
314 interspecific brood parasitism (see for review in Guigueno & Sealy 2012).

315 Rejection rates of green and orange eggs, whether in the minority or in the majority of  
316 the clutch, were similar when combined with other eggs (natural or blue). However, when in  
317 the presence of each other, the rejection rates for the green eggs were higher than expected  
318 from the other combinations for single and green eggs, but not for the orange eggs (Fig. 2).

319 This similarity of rejection rates of both the minority green and the majority orange eggs  
320 implies that the particular colours of majority vs. minority eggs interact in a previously  
321 unknown manner to generate egg rejection behaviours. Results such as these may form the  
322 basis of future physiological studies on the hypotheses about the opponency-based process of  
323 the avian tetrachromatic vision (Vorobyev & Osorio 1998) in hosts' egg discrimination.

324 The most typical case of parasitized clutches is when the nest contains several host  
325 eggs and one parasitic egg, generating a discordant clutch (e.g. in *Molothrus* cowbirds;  
326 Hauber 2001; in *Cuculus* cuckoos: Moskát & Hauber 2007). Nevertheless, parasitic eggs  
327 could also be the majority egg type in a clutch in areas with locally high rates of multiple  
328 parasitism (Moskát et al. 2009; Stevens et al. 2013). Our experiments tested the influence of  
329 majority egg colours on the rejection of minority egg colours, and showed that the ejection of  
330 the minority egg was increased when it belonged to a less mimetic colour relative to the  
331 majority eggs. A previous experimental study, also on the great reed warbler, already showed  
332 that the successful ejection of an easily recognisable (i.e. non-mimetic) egg type helped the  
333 ejection of another egg type (moderately mimetic) which was otherwise more difficult to  
334 recognize by these hosts (Hauber et al. 2006). Egg rejection behaviours may have been due to  
335 observational learning to recognise foreign eggs during egg laying in that previous study, but  
336 here we excluded this possibility by starting our treatments with dyed eggs at clutch  
337 completion. Future studies should clarify how different host species solve the task of own vs.  
338 foreign egg discrimination in the face of intrinsic vs. extrinsic sources of variation in the  
339 homogeneity of (non-) parasitized clutch appearance (e.g. egg arrangement in the nest:  
340 Poláčiková et al. 2013).

341 We conclude that great reed warblers' parasitic egg discrimination is affected by the  
342 appearance of the whole clutch, not only by the phenotype of the parasitic egg(s) alone. This  
343 finding probably has more relevance for systems where parasites repeatedly target or multiple  
344 parasites lay in hosts nests (Hauber et al. 2012); for example, with multiple cuckoo eggs laid  
345 by the same or different female cuckoos (Wyllie 1981), which is common in our great reed  
346 warbler population (Moskát et al. 2009). Although these hosts primarily recognize foreign  
347 eggs by a memory-template based mechanism (Bán et al. 2013), they also rely on a  
348 discordancy mechanism (Moskát et al. 2010; this study). Here we manipulated the extent of  
349 discordancy by using differently mimetic artificial egg colours, to understand this duality in  
350 the hosts' decision mechanisms. In concordance with our previous results (Bán et al. 2013),  
351 we revealed that discordancy in foreign egg recognition of this cuckoo host species functions  
352 not as a primary recognition mechanism, but its effect is contextual, and induces or prevents

353 egg discrimination in the context of more (or less) mimetic egg colours present in the nest.  
354 These results suggest that non-mimetic parasitic eggs may help to recognize mimetic parasitic  
355 eggs in the clutch. In a population with high rates of multiple parasitism, often by different  
356 females, this recognition mechanism may provide a novel route to accelerate the evolution of  
357 egg colour mimicry of host eggs by its specialist parasites, so that differently mimetic parasite  
358 eggs are less likely to occur in the same nest (Brooker et al. 1990; Spottiswoode 2013).

359         Previous studies in our great reed warbler population revealed that multiple cuckoo  
360 eggs were typically laid by different cuckoo females and cuckoos did not preferentially lay in  
361 nests with already present cuckoo eggs; they also removed one already present egg from nest  
362 at random (Moskát & Honza 2002). However, laying cuckoos may select host nests with  
363 better match between host and parasitic eggs than expected by chance (Avilés et al. 2006;  
364 Cherry et al. 2007b; Honza et al. 2014). This process may result in better mimicry of the host  
365 eggs by the parasite (Igic et al. 2012), yielding less heterogeneous clutches, even in multiple  
366 parasitism, and selecting for further fine-tuning of the sensory and cognitive rules used by  
367 hosts to recognize foreign eggs, as seen in our results here. Future studies should aim to reveal  
368 whether template-based recognition enhances the recognition of foreign eggs detected through  
369 discordancy, and how these two processes interact with perceived mimicry and enhance or  
370 interfere with each other egg to yield recognition decisions (Stevens et al. 2013), eventually,  
371 to generate the naturally and experimentally elicited rejection behaviours at level of the  
372 individual hosts.

373

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381

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561 Table 1. Results of the most parsimonious models for estimating the impact of colour-  
 562 dependent discordancy on egg rejection by great reed warbler.  $\alpha = 0.05$ , significant  $P$  values  
 563 are underlined for added emphasis. 'Response' is the reaction of hosts to the experimental  
 564 parasitism, either acceptance or ejection. 'Treatment' refers to experimental manipulations,  
 565 when one egg in the clutch ("minority") was dyed green or orange, and the rest of the eggs  
 566 ("majority") dyed a different colour (either orange, green or blue) or were left in their natural  
 567 state. 'Laydate' denotes the number of days passed after the appearance of the first egg,  
 568 'clsize' is clutch size; and offset is the dispersion correction parameter.  
 569

<i>Model (dataset, type of response)</i>	<i>Estimates</i>	<i>SE</i>	<i>z</i>	<i>P</i>
<b>Minority, response</b>				
~treatment+laydate+offset(log(clsize+1))				
Intercept ("1 green and 4 blue eggs")	-2.99	1.03	-2.09	<u>0.003</u>
"1 green and 4 natural eggs"	-0.1	1.09	-0.09	0.92
"1 green and 4 orange eggs"	1.93	0.97	1.98	<u>0.047</u>
"1 orange and 4 natural eggs"	2.84	0.94	3.02	<u>0.002</u>
"1 orange and 4 blue eggs"	2.42	0.97	2.49	<u>0.012</u>
"1 orange and 4 green eggs"	2.11	0.95	2.21	<u>0.026</u>
Laydate	-0.02	0.04	-0.72	0.47
<b>Minority, no. of eggs ejected</b>				
~treatment+laydate+offset(log(clsize+1))				
Intercept ("1 green and 4 blue eggs")	-3.43	0.85	-3.99	<0.001
"1 green and 4 natural eggs"	-0.14	1.01	-0.14	0.88
"1 green and 4 orange eggs"	1.28	0.819	1.56	0.11
"1 orange and 4 natural eggs"	1.61	0.76	2.12	<u>0.03</u>
"1 orange and 4 blue eggs"	1.48	0.786	1.88	<u>0.05</u>
"1 orange and 4 green eggs"	1.35	0.796	1.7	0.088
Laydate	-0.013	0.02	-0.46	0.63
<b>Majority, response</b>				
~treatment+offset(log(clsize+1))				
Intercept ("1 orange and 4 green eggs")	-2.89	0.57	-5.02	<0.001
"1 green and 4 orange eggs"	1.35	0.76	1.77	0.076
<b>Majority, no. of eggs ejected</b>				

~treatment+offset(log(clsiz+1))

Intercept ("1 orange and 4 green eggs")	-2.009	0.27	-7.24	<0.001
"1 green and 4 orange eggs"	1.008	0.32	3.08	0.002

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571

572 Table 2. Multiple comparisons for treatment effect (with Tukey contrast matrices) estimating  
 573 the discordance by egg rejection for Reed Warbler;  $\alpha = 0.05$ , significant  $P$  values are  
 574 underlined for added emphasis. 'Response' is the reaction of hosts to the experimental  
 575 parasitism, either acceptance or ejection. 'Treatment' means experimental treatments, when  
 576 one egg in the clutch ("minority") was dyed green or orange, and the rest of the eggs  
 577 ("majority") to a different colour (either orange, green or blue) or were left in their original,  
 578 natural state.  
 579

<i>Comparisons (dataset, type of response)</i>	<i>Estimates</i>	<i>S.E.</i>	<i>Z</i>	<i>P</i>
<b>Minority, response</b>				
"1 green and 4 natural eggs" - "1 green and 4 blue eggs"	-0.1022	1.0994	-0.093	1.000
"1 green and 4 natural eggs" - "1 green and 4 orange eggs"	2.0395	0.9151	2.229	0.220
"1 green and 4 natural eggs" - "1 orange and 4 natural eggs"	2.9448	0.9207	3.198	<u>0.017</u>
"1 green and 4 natural eggs" - "1 orange and 4 blue eggs"	2.5245	0.9422	2.679	0.077
"1 green and 4 natural eggs" - "1 orange and 4 green eggs"	2.2137	0.9094	2.434	0.141
"1 green and 4 blue eggs" - "1 green and 4 orange eggs"	1.9374	0.9777	1.982	0.347
"1 green and 4 blue eggs" - "1 orange and 4 natural eggs"	2.8426	0.9412	3.020	<u>0.029</u>
"1 green and 4 blue eggs" - "1 orange and 4 blue eggs"	2.4223	0.9701	2.497	0.122
"1 green and 4 blue eggs" - "1 orange and 4 green eggs"	2.1115	0.9514	2.219	0.224
"1 green and 4 orange eggs" - "1 orange and 4 natural eggs"	0.9052	0.7483	1.210	0.829
"1 green and 4 orange eggs" - "1 orange and 4 blue eggs"	0.4849	0.7689	0.631	0.988
"1 green and 4 orange eggs" - "1 orange and 4 green eggs"	0.1742	0.7187	0.242	0.999
"1 orange and 4 natural eggs" - "1 orange and 4 blue eggs"	0.4203	0.7677	0.547	0.994
"1 orange and 4 natural eggs" - "1 orange and 4 green eggs"	0.7311	0.7326	0.998	0.917
"1 orange and 4 blue eggs" - "1 orange and 4 green eggs"	-0.3108	0.7581	-0.410	0.999
<b>Minority, no. of eggs ejected</b>				
"1 green and 4 natural eggs" - "1 green and 4 blue eggs"	-0.1496	1.0127	-0.148	1
"1 green and 4 natural eggs" - "1 green and 4 orange eggs"	1.4299	0.7924	1.804	0.441
"1 green and 4 natural eggs" - "1 orange and 4 natural eggs"	1.7651	0.7592	2.325	0.17
"1 green and 4 natural eggs" - "1 orange and 4 blue eggs"	1.6332	0.7854	2.079	0.28
"1 green and 4 natural eggs" - "1 orange and 4 green eggs"	1.5054	0.7817	1.926	0.366
"1 green and 4 blue eggs" - "1 green and 4 orange eggs"	1.2803	0.8193	1.563	0.603
"1 green and 4 blue eggs" - "1 orange and 4 natural eggs"	1.6155	0.7611	2.123	0.258
"1 green and 4 blue eggs" - "1 orange and 4 blue eggs"	1.4836	0.7861	1.887	0.389
"1 green and 4 blue eggs" - "1 orange and 4 green eggs"	1.3558	0.7961	1.703	0.508
"1 green and 4 orange eggs" - "1 orange and 4 natural eggs"	0.3352	0.4608	0.727	0.976

"1 green and 4 orange eggs" - "1 orange and 4 blue eggs"	0.2033	0.5035	0.404	0.998
"1 green and 4 orange eggs" - "1 orange and 4 green eggs"	0.0755	0.4902	0.154	1
"1 orange and 4 natural eggs" - "1 orange and 4 blue eggs"	0.1319	0.4273	0.309	1
"1 orange and 4 natural eggs" - "1 orange and 4 green eggs"	0.2597	0.4317	0.602	0.99
"1 orange and 4 blue eggs" - "1 orange and 4 green eggs"	-0.1278	0.4762	-0.268	1

**Majority, response**

"1 green and 4 orange eggs" - "1 orange and 4 green eggs"	1.35	0.76	1.77	0.076
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**Majority, no. of eggs ejected**

"1 green and 4 orange eggs" - "1 orange and 4 green eggs"	1.008	0.32	3.08	<u>0.002</u>
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