

## Foreign egg retention by avian hosts in repeated brood parasitism: why do rejecters accept?

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**Abstract** Great reed warblers (*Acrocephalus arundinaceus*) are frequently parasitized by egg-mimetic common cuckoos (*Cuculus canorus*) in Hungary, and these hosts reject about a third of parasitic eggs. The timing of parasitism is important, in that the probability of rejection decreases with advancing breeding stages in this host. Also, egg rejection is more common when a clutch is parasitized by a single foreign egg, compared to parasitism by multiple eggs. We repeatedly parasitized great reed warbler clutches with moderately mimetic foreign eggs, either with (1) one foreign egg (single

parasitism) and, after 3 days, by all foreign eggs (multiple parasitism), or (2) all foreign eggs and, 3 days later, by only one foreign egg. Hosts ejected 26–53 % of the parasitic eggs in the first stage of the repeated parasitism, but almost all eggs were accepted in the second stage, irrespective of whether the clutch was singly or multiply parasitized. Video-taping of the behavioural responses of hosts to experimental parasitism revealed no evidence for sensory constraints on foreign-egg recognition, because hosts recognized and pecked the parasitic eggs as frequently in the second stage of repeated parasitism, as they did in the first stage. We suggest that the relative timing of parasitism (laying vs. incubation stage), rather than learning to accept earlier-laid foreign eggs, results in higher acceptance rates of cuckoo eggs in repeated parasitism, because there is decreasing natural cuckoo parasitism on this host species and, hence, less need for antiparasitic defences, with the advancing stages of breeding.

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### Introduction

Parental investment is costly (Clutton-Brock 1991), and hosts of obligate brood parasites suffer fitness losses by provisioning unrelated young (Davies 2000, 2011). To avoid detection and rejection by hosts, avian brood parasites may locally specialize on a host species, and evolve eggs or young closely resembling those of the hosts (Kilner and Langmore 2011). Some of the best-known examples of brood parasites' adaptations to hosts can be found in common cuckoos (*Cuculus canorus*; Moksnes and Røskaft 1995; Higuchi 1998; Davies 2000; hereafter: the cuckoo), which lay mimetically coloured and patterned eggs (e.g. Brooke and Davies 1988; Antonov

56 et al. 2010; Stoddard and Stevens 2010, 2011; Igic et al. 2012;  
57 Moskát et al. 2012). In a co-evolutionary arms race, hosts  
58 respond to parasitic egg mimicry by evolving ever more fine-  
59 tuned abilities of discrimination between own and foreign  
60 eggs, and rejecting parasitic eggs by egg ejection, egg burial,  
61 or nest desertion (Rothstein 1975; Davies and Brooke 1988;  
62 Moksnes et al. 1991; Lotem et al. 1995; Hosoi and Rothstein  
63 2000; Sealy and Underwood 2012).

64 Accepting a parasitic egg is particularly costly for hosts of  
65 the common cuckoo, because the hatchling parasite evicts all  
66 host eggs and nestmates (Anderson et al. 2009), thereby  
67 annihilating any fitness benefit gained from that reproductive  
68 attempt. Accordingly, the cuckoo egg must be eliminated by  
69 the host prior to hatching, either during the egg laying or the  
70 incubation period. Despite the clear benefits of rejecting cuck-  
71 oo eggs, many hosts do not do so; they accept the parasitic egg  
72 and eventually face the loss of their reproductive attempt,  
73 including cases where the physical characteristics of the eggs  
74 prevent rejection by ejection (Antonov et al. 2009; Krüger  
75 2011). More puzzling is the scenario when hosts clearly  
76 possess the sensory and morphological adaptations to recog-  
77 nize and remove foreign eggs (Hauber et al. 2006; Moskát and  
78 Hauber 2007), yet they do not do so.

79 Our study aimed to explore the interactions between para-  
80 sitism pressures, breeding stages, and cognitive dimensions,  
81 to examine why hosts do not use their ability to rescue their  
82 own breeding attempt by rejecting cuckoo eggs in a heavily  
83 parasitized population of the great reed warbler (*Acrocephalus*  
84 *arundinaceus*). We designed a set of treatments to study hosts'  
85 responses to parasitism under several conditions, including  
86 single, multiple, and repeated parasitism (Hauber et al. 2004;  
87 Samas et al. 2011), while also comparing the effects of breed-  
88 ing stage (laying vs. incubation stage) and prior experience  
89 with foreign eggs (Hauber et al. 2006). We assessed differ-  
90 ences in egg discrimination decisions on the basis of the  
91 frequency of egg rejection behaviours in response to our  
92 experimental parasitism (e.g. Davies and Brooke 1988;  
93 Moksnes et al. 1991; Hale and Briskie 2007; Begum et al.  
94 2012; de la Colina et al. 2012). We also used video recordings  
95 of host behaviours at the nest after the experimental manipu-  
96 lation, to record any pecking of eggs by hosts, which can be  
97 regarded as an the indicator of foreign egg recognition (Soler  
98 et al. 2002; Antonov et al. 2008, 2009; Honza et al. 2007;  
99 Pozgayová et al. 2011). We examined the dynamics of the  
100 acceptance of the parasitic eggs in great reed warblers, regard-  
101 ing the temporal progress of the breeding cycle (laying vs.  
102 incubation nesting stages), and tested which cognitive rules  
103 allow or limit foreign egg recognition, by limiting the possi-  
104 bility to use discordancy or template-based recognition (sensu  
105 Moskát et al. 2010; Bán et al. 2013).

106 Soon after the onset of our study (during the first year), we  
107 found that hosts showed almost no rejection toward experi-  
108 mental parasitic eggs in repeated parasitism (i.e., parasitism

with a single egg of the same nest, spaced several days apart; 109  
see below). Therefore, we generated two ad hoc hypotheses, 110  
and tested their specific predictions, regarding decreasing 111  
rejection rates with temporal progress across the breeding 112  
stages, from laying to incubation. First, following the hypoth- 113  
esis by Rothstein 1976 (see also Davies and Brooke 1989, and 114  
Moksnes and Røskaft 1991), we hypothesized that hosts may 115  
modulate the intensity of their egg discrimination according to 116  
changes in the risk of parasitism during the nesting stages. 117  
Accordingly, we predicted lower rejection rates with 118  
progressing incubation in single parasitism, irrespective of 119  
prior experience to parasitism, during periods of lower para- 120  
sitism pressure and costs, i.e., in the later breeding stages (e.g., 121  
few to no cuckoo eggs laid during the incubation vs. more 122  
cuckoo eggs laid during the laying stage, Moskát 2005, as 123  
later laid cuckoo eggs have a lower chance to hatch, Birkhead 124  
et al. 2011). Second, we hypothesized that hosts which did not 125  
reject parasitic eggs in the first stage of the experiment, may 126  
have learned the attributes of the experimental egg as one of 127  
their own eggs, so later these same hosts might consider the 128  
second set of foreign egg(s) in the experimental repeated 129  
parasitism, as their own, and accept it. Therefore, we predicted 130  
lower rejection rates of the foreign eggs in the second stage of 131  
the repeated parasitism treatment, compared to rejection rates 132  
of foreign eggs in single parasitism during the later stage of the 133  
breeding cycle (i.e. incubation). 134

## 135 Methods

### 136 Study site and species

137 The research was performed ca. 50 km south of Budapest, 138  
Hungary, in the surroundings of Apaj village (47°07'N; 139  
19°06'E). We searched for the nests of great reed warblers in 140  
2–3 m wide reed beds (*Phragmites australis*) on both sides of 141  
narrow irrigation channels, covering the same segments once or 142  
twice a week, from mid May until late June in 2010 and 2012. 143  
This host species is heavily parasitized by common cuckoos in 144  
this area (ca. 40–65 %; Moskát et al. 2012). We used naturally 145  
non-parasitized nests for our experiments, and nests that were 146  
parasitized during our monitoring period, were excluded from 147  
the analyses. At this study site, great reed warblers normally 148  
breed once in a season (our unpublished result), but replacement 149  
clutches may occur in the same territory, as a consequence of 150  
predation. We did not use more than one nest within a territory to 151  
avoid pseudo-replication. Individual colour banding of about half 152  
of the adult breeding birds in 2010 also helped to avoid pseudo- 153  
replication. Only the females are responsible for egg rejection in 154  
this species (Pozgayová et al. 2009; Trnka et al. 2012).

155 In our study area, cuckoo eggs show extensive variation in 156  
colour and maculation (e.g., Cherry et al. 2007; Moskát et al. 157  
2012), but the size of a cuckoo egg is similar to a great reed

158 warbler egg (Hargitai et al. 2010), although they are different in  
 159 shape (Bán et al. 2011). Therefore, we used painted host eggs for  
 160 experimental parasitism, instead of introducing model eggs into  
 161 host nests (Zölei et al. 2012). We used yellow highlighter pens  
 162 (Schwan Stabilo Boss art No. 7024; for spectral data, see Bán  
 163 et al. 2013) for dyeing the eggs, causing a green-yellowish coat  
 164 covering the entire eggs' surface. Although this highlighter's dye  
 165 was water-soluble, it typically persisted in coating the shells for  
 166 the full 3- or 6-day monitoring periods. At about 10 % of the  
 167 nests, small patches of dye were rubbed off the eggshells and  
 168 made it necessary to repaint during one of the daily nest checks.  
 169 Great reed warblers rejected this egg type in single experimental  
 170 parasitism at a similar frequency as real cuckoo eggs in  
 171 natural parasitism (50 % rejection rate;  $n=12$  rejection  
 172 of yellow dyed eggs in single experimental parasitism; Bán  
 173 et al. 2013 vs. 40 % of real cuckoo eggs in single parasitism;  
 174  $n=45$ ; Moskát et al. 2009).

175 **Experimental treatments**

176 In our experiments, we simulated two types of natural cuckoo  
 177 parasitism: (1) single parasitism with one foreign egg in a  
 178 clutch, which can be regarded the most common case of brood  
 179 parasitism across most species and populations (Davies 2000),  
 180 or (2) Multiple parasitism (Moskát et al. 2009). In theory,  
 181 multiple parasitism applies for all cases with more than one  
 182 parasitic egg in a clutch, but in our study, multiple parasitism  
 183 was simulated with all eggs being parasitic. This experimental  
 184 design is useful to test the "template-based" recognition mech-  
 185 anism for foreign egg rejection (Moskát et al. 2010; Bán et al.  
 186 2013), because the alternative mechanism, "discordancy"  
 187 (Rensch 1925; but see Rothstein 1974; Sealy and  
 188 Underwood 2012), cannot be applied by hosts when all eggs  
 189 in clutch belong to the same, albeit foreign, egg phenotype.  
 190 This experimental design is also conceptually similar to the  
 191 case when the hosts' clutch size is only one, and it contains just  
 192 the parasitic egg (Lahti and Lahti 2002), or to those cases  
 193 during the early stages of the laying cycle, when the cuckoo  
 194 lays before the onset of the hosts' incubation (Sealy 1995), or  
 195 when the parasite replaces the host's first egg in the clutch  
 196 (Moskát and Hauber 2007). In turn, we called the type of  
 197 experimental parasitism, when foreign eggs are introduced  
 198 into the nest at the same point in time, "one-time parasitism";  
 199 in turn, when two different parasitism events follow each other  
 200 at a nest, separated by 1 or more days (e.g., a single parasitism  
 201 and, after 3 days, multiple parasitism, or vice versa), we call  
 202 this type of parasitism "repeated parasitism".

203 *Experiment 1 (repeated parasitism)*

204 In this experiment, we studied how the same individuals  
 205 respond to single and multiple parasitism when the two treat-  
 206 ments follow one another (termed "repeated parasitism").

*Treatment 1a* On the fifth day of laying (denoted by 5d), when  
 the clutch contained five eggs, we chose one host egg ran-  
 domly from the clutch and dyed it yellow. If clutch size was  
 four, we also started our experiment on the fifth day as in the  
 case when clutch size was five, as previous studies revealed no  
 effect of clutch size on great reed warblers' egg rejection (e.g.,  
 Moskát et al. 2010). Our manipulation typically altered the  
 original position of all eggs in the clutch (Polaciková et al.  
 2013). Experimental nests were monitored daily on 3 consec-  
 utive days in each categories of Experiment 1. Host response  
 to the foreign egg was categorized as acceptance if the dyed  
 egg was still in the clutch and looked undamaged. If the eggs  
 were cold, and were not rotated for 2 days (for details,  
 see Bán et al. 2013), the hosts' response was categorised  
 as nest desertion. If the eggs were incubated, but the  
 parasitic egg was missing, the outcome of the experiment was  
 considered as egg ejection.

*Treatment 1b* Three days after treatment 1a began, at 8d, all  
 host eggs were dyed yellow. An ejection was detected if at  
 least one painted egg was missing from the nest.

*Treatment 2a* As in treatment 1b, but all host eggs in the  
 clutch were dyed yellow at 5d.

*Treatment 2b* After 3 days of monitoring treatment 2a, at 8d,  
 all dyed host eggs except one was cleaned off of yellow dye,  
 by rinsing the eggs in water, and then one egg was repainted  
 yellow.

*Control* No eggs in the control nests were dyed, but the eggs  
 were inspected and handled similarly to those in the experi-  
 mental nests.

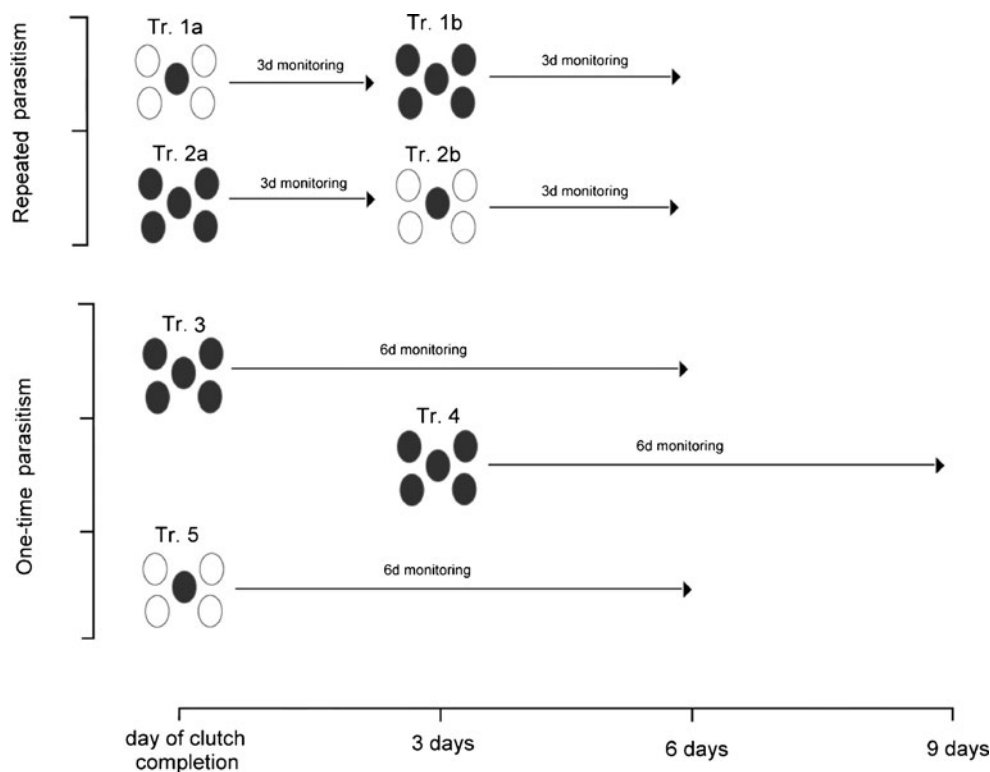
All clutch manipulations in this experiment were carried  
 out in 2010 and 2012. The schematic representation of this  
 experiment's treatments is illustrated in Fig. 1.

*Experiment 2 (one-time parasitism)*

As Experiment 1 yielded unpredicted results in the second,  
 repeated parasitism portion of our treatments (namely that we  
 detected many fewer rejections toward the foreign eggs in  
 treatments 1b and 2b; see Results for details), we designed  
 and conducted a new experiment to test alternative explana-  
 tions for the patterns of egg rejection documented in  
 Experiment 1.

*Treatment 3* All host eggs were dyed yellow at 5d. This is the  
 same manipulation as in treatment 2a, but the monitoring  
 period was 6 days post manipulation (which is the standard  
 in cuckoo-host egg rejection studies: Grim et al. 2011), instead  
 of 3 days. No other treatment (i.e., repeated parasitism)  
 followed this one.

**Fig. 1** The schematic representation of treatments (*Tr.*) applied in repeated parasitisms (Experiment 1) and non-repeated parasitisms (Experiment 2). White eggs denote the host's own eggs, and dark eggs denote experimental parasitic eggs. Monitoring periods after parasitism (3 or 6 days) are also shown, whereas hatching time of host eggs is about 11–12 days after clutch completion (our unpublished result). Clutch size shown in the figure is five, which is the modal clutch size of great reed warblers in our population. However, some clutches contained four or six eggs, which did not affect rejections as our linear model revealed (see Results for more details)



253 *Treatment 4* As above in treatment 3, but manipulations were  
 254 done at 8d. Again, this treatment is similar to treatment 1b, but  
 255 no manipulation was done preceding this one, and the moni-  
 256 toring period was 6 days post manipulation.

257 *Treatment 5* We used data on one-time parasitism with one  
 258 host egg dyed yellow, started at 5d, and with a 6-day moni-  
 259 toring period to evaluate to effect of the length of monitoring  
 260 period (3 or 6 days) on this host's egg rejection rates.

261 *Control* As in Experiment 1.

262 Experiment 2 was carried out in 2012, but for treatment 5  
 263 we also included our published results on egg rejection be-  
 264 haviours from recent years (Bán et al. 2013).

265 Video recordings

266 In 2012, we documented host behaviours at the nest, imme-  
 267 diately after the manipulation of their clutches using five  
 268 digital camcorders (Samsung HMX-H300 cameras using 32-  
 269 GB Samsung SDHC memory cards for storage, with the  
 270 options of 1860/60i resolution and 1920x1080 video quality).  
 271 We positioned each camera 4–5 m from the host nests on  
 272 tripods, and left them in place for 15–20 min, before recording  
 273 started to allow habituation of the parents. To avoid human  
 274 disturbance, we left the immediate vicinity of the camera  
 275 (>50 m) to reduce observer disturbance during recording.  
 276 Recording sessions typically lasted more than 2 h (2.30±

0.023 h [mean±SE], measured from first arrival of the female  
 277 bird). We recorded host behaviours in three different treatment  
 278 categories in 2012: (1) treatment 1b, (2) treatment 3, and (3)  
 279 control.  
 280

281 As we were interested in host behaviour occurring just after  
 282 experimental parasitism, we quantified the following elements  
 283 of host behaviour: (1) "pecking" (number of pecks directed at  
 284 the clutch/h); (2) "inspection" (Fig. 2; seconds of time spent on  
 285 looking at the clutch/h); (3) "sitting" (seconds of time spent on  
 286 sitting on the eggs/h), and (4) "rotation" (seconds of time spent  
 287 on rotating the eggs/h).

288 Statistical analysis

289 Generalized (logistic) linear mixed-effect models (GLMM;  
 290 Bolker et al. 2009; Nakagawa and Hauber 2011) were used  
 291 to assess the relationship between explanatory variables and  
 292 the ejection events of single eggs, using a binary response  
 293 variable (where 0 or 1 denotes acceptance or rejection, respec-  
 294 tively). Nest identity was included as a random effect to  
 295 account for non-independence of treatments at the same nest  
 296 in repeated parasitism. We used the following explanatory  
 297 variables in the models: treatment, start of egg laying (i.e.,  
 298 first egg laying date), and the number of eggs per nest. Two  
 299 model types were tested, and compared to each other, as well  
 300 as to the null model, by a log likelihood ratio test and the  
 301 Akaike Information Criterion (AIC): (1) the simple effect  
 302 model, where the impact of the explanatory variables was





**Fig. 2** A great reed warbler is looking at its clutch (*above*), and ejecting a parasitic egg by puncture ejection (*below*). Both nests were experimentally multiply parasitized by dyeing yellow all of the host's own eggs with a highlighter pen. This host species rejects such yellow-dyed experimental eggs (Bán et al. 2013) at a similar frequency to rejecting real common cuckoo eggs, when the clutch is parasitized in the egg laying stage (Moskát et al. 2009)

303 considered; (2) the interaction model, where a "number of  
 304 days"× treatment interaction term was added to the simple  
 305 effect model. The most parsimonious model was selected to  
 306 analyze the differences in the responses; the simple effect  
 307 model provided the better fit to the dataset (for details, see  
 308 Table I in the [Electronic Supplementary Material](#)).

309 Differences among the levels of the included explanatory  
 310 variables were evaluated by multiple comparisons, after first  
 311 applying a single-argument analysis of variance  
 312 (ANOVA) for the tested model. The model estimates  
 313 were obtained using a maximum likelihood method,  
 314 and the diagnostics included the graphical output for  
 315 the model residuals. We estimated the model parameters  
 316 by using the *nlme* (Pinheiro et al. 2012) and *lme4* packages  
 317 (Zeileis and Hothorn 2002) for likelihood tests in R 2.14.0 (R  
 318 Development Core Team 2012).

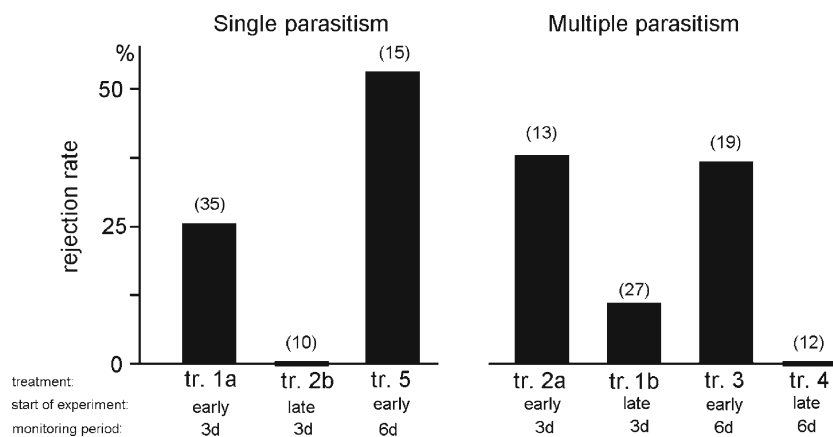
We compared videotaped host behaviours at nests by ana- 319  
 lyzing each of the following variables: egg pecking, clutch 320  
 inspection, sitting and rotation. The ordinary least square 321  
 mean method was used to estimate the behavioural rates of 322  
 egg pecking, clutch inspection, sitting and rotation per unit 323  
 time. These responses were tested between treatments 1b, 3 324  
 and the controls by a single-argument ANOVA (permutational 325  
 ANOVA), where the number of iterations was taken to gen- 326  
 erate exact P values (Box 1988). 327

**Results** 328

No egg was rejected from any of the control nests which had 329  
 unmanipulated host eggs ( $n=27$ ). In turn, we found the 330  
 highest rejection rate (53 %) of the parasitic egg in treatment 331  
 5, when single parasitism was started at clutch completion 332  
 with 6d monitoring period (cf. Fig. 3). Hosts typically ejected 333  
 the parasitic egg(s) (altogether from 25 nests), but in five cases 334  
 of three treatments hosts deserted the parasitized clutch (de- 335  
 sertions/rejections: 2/9, 1/5 and 2/7 nests in treatments 1a, 2a 336  
 and 3, respectively). Hosts ejected 1–5 eggs from multiple 337  
 parasitized nests (mean:  $3.25 \text{ eggs} \pm 0.675 \text{ SE}$  in treatments 2a 338  
 and 3). In one case, in treatment 1a, host ejected the single 339  
 parasitic egg together with an own natural egg (ejection cost). 340  
 Latencies of egg rejections were similar in corresponding 341  
 pairs of treatments regarding the 3d or 6d monitoring periods, 342  
 both in single and multiple parasitisms (single parasitism: 343  
 treatment 1a,  $1.43 \pm 0.202 \text{ days}$  [mean±SE]; treatment 5, 344  
 $2.25 \pm 0.648 \text{ days}$ ; multiple parasitism: treatment 2a,  $2.50 \pm$  345  
 $0.500 \text{ days}$ ; treatment 3,  $1.80 \pm 0.837 \text{ days}$ ). The difference 346  
 proved to be non-significant both between latencies in single 347  
 parasitism treatments (Mann–Whitney  $U=23.00$ ,  $P=0.613$ ) 348  
 and multiple parasitism treatments (Mann–Whitney  $U=5.50$ , 349  
 $P=0.286$ ). 350

Our linear model (GLMM) for the results from the different 351  
 treatments in multiple parasitism revealed that the frequency 352  
 of egg rejections (Fig. 3) was affected by treatment and the 353  
 onset time (5d vs. 8d) of the experiment (Table 1). Egg 354  
 rejection was elicited less frequently in treatment 4 than either 355  
 in treatment 2a or 3 ( $B=0.255$ ,  $SE=0.111$ ,  $t_{65}=2.285$ , 356  
 $P=0.023$ ;  $B=0.226$ ,  $SE=0.128$ ,  $t_{65}=1.76$ ,  $P=0.008$ , respec- 357  
 tively), but was statistically similar to treatment 1b ( $B=0.073$ , 358  
 $SE=0.13$ ,  $t_{65}=-0.563$ ,  $P=0.575$ ). Rejections showed a 359  
 unimodal pattern according to the calendar date of the onset 360  
 of laying of experimental nests throughout the breeding sea- 361  
 son, with a maximum in the middle of the study period and 362  
 with tails of lower frequencies earlier and later in the breeding 363  
 season;  $B=-0.016$ ,  $SE=0.005$ ,  $t_{65}=-2.836$ ,  $P=0.006$ ). The 364  
 number of eggs in clutches had no effect on egg rejections 365  
 ( $B=-0.056$ ,  $SE=0.079$ ,  $t_{65}=-0.716$ ,  $P=0.476$ ). 366

Video analyses revealed similar behaviours of hosts related 367  
 to the different treatments (Fig. 4 and Table 2). We recorded 368



**Fig. 3** Rejection rates of experimental eggs in artificial parasitism of the great reed warbler with moderately mimetic yellow-dyed own eggs (*tr. 1a* treatment 1a, *tr. 1b* treatment 1b, *tr. 2a* treatment 2a, *tr. 2b* treatment 2b, *tr. 3* treatment 3, *tr. 4* treatment 4). In single parasitism the clutch contained one experimental egg and four host eggs; in multiple parasitism

the clutch contained five experimental eggs; *early* early parasitism at clutch completion, *late* late parasitism 3 days after clutch completion. Nests were monitored either for 3 days (3d) or 6 days (6d) after experiment started

369 egg pecking at just less than half of the nests (Fig. 4a). It was  
 370 documented at 30 % of nests with experimental parasitism  
 371 at 5d (treatment 3; 3/10), and 50 % of nests with parasitism  
 372 at 8d (in treatment 1b; 4/8). Interestingly, we also found  
 373 egg pecking behaviour in 38 % of control nests, where no  
 374 parasitic eggs were present (3/8). There were generally no  
 375 significant differences in the patterns of the three  
 376 different aspects of host behaviours between the differ-  
 377 ent treatments and controls (Table 2), except for egg  
 378 rotation, but that was due to an outlier data point (Grub  
 379 test:  $G=3.6653$ ,  $U=0.441$ ,  $P<0.001$ ; Fig. 1 in the  
 380 [Electronic Supplementary Material](#)); after the removal  
 381 of the outlier (Grub test:  $G=1.919$ ,  $U=0.840$ ,  
 382  $P=0.597$ ), there were no significant differences between  
 383 the treatments and controls (Table 2). Although egg  
 384 pecking was not significantly different among the three  
 385 treatments ( $P=0.068$ ; Table 2), contrary to predictions,  
 386 the pattern of mean pecking rate showed in fact higher  
 387 values in late parasitism (treatment 1b) and was  $7.58 \pm$   
 388  $5.485$ , in contrast with lower values in early parasitism  
 389 (treatment 3:  $0.48 \pm 0.255$ ) and in the control ( $0.42 \pm 0.264$ ).

**Discussion**

390

Our results, from repeated experimental parasitism on great  
 reed warblers, revealed an unusual pattern of antiparasitic  
 behaviours: hosts showed intermediate rejection rates (26–  
 53 %) toward one or more parasitic eggs in a clutch at the  
 first stage of parasitism, but typically showed no rejection at  
 the second stage, following a 3-day monitoring period after  
 the first parasitism. Previous studies suggested that hosts may  
 learn their own eggs during their first laying attempts (e.g.,  
 Rothstein 1975; Lotem et al. 1995; Stokke et al. 2007;  
 Strausberger and Rothstein 2009), and several theoretical  
 models on egg rejection behaviour also incorporated a  
 learning-based egg recognition component (Rodriguez-  
 Gironés and Lotem 1999; Stokke et al. 2007). However,  
 recent studies demonstrate prominent interannual variation  
 in coloration of eggs laid by the same hosts across different  
 years; consequently, individual hosts should learn their own  
 eggs' phenotype in each year or in each egg laying cycle  
 (Honza et al. 2012; Wheelwright et al. 2012; Soler et al.  
 2013). Yet, our results did not support this clutch-learning  
 hypothesis (Hauber et al. 2004) whereby hosts may learn the  
 experimental parasitic eggs' phenotype to consider it as their  
 own eggs during the first instance of parasitism, and later they  
 accept it in the second parasitism event. We found the same  
 result of acceptance when experimental parasitism was ap-  
 plied only once, at the later time point. Specifically, these data  
 imply that acceptance of experimental parasitism during the  
 second instance of repeated parasitism is not caused by  
 misimprinting on the parasitic egg(s), as one of the host's  
 own egg(s) during the first instance of the repeated parasitism  
 experiment.

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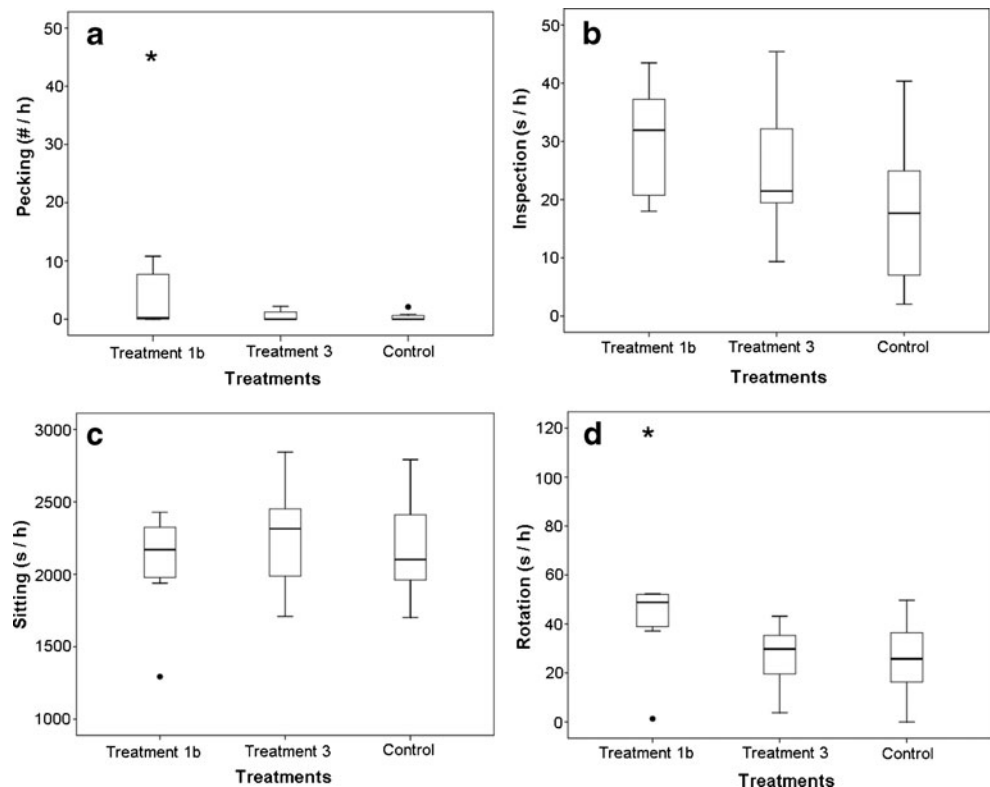
Video-taped evidence on host behaviours at the nest, re-  
 corded just after the experimental parasitism, revealed that,

421  
422

t1.1 **Table 1** Results of generalized linear mixed models (GLMM) of rejection rates of experimental eggs by great reed warblers with treatment (treatments 1b, 2a, 3 and 4), timing of experiment, and clutch size as predictor variables

t1.2		<i>df</i>	<i>F</i>	<i>P</i>
t1.3	Intercept	1,65	22.814	<0.0001
t1.4	Treatment	3,65	3.998	0.011
t1.5	Timing of exp.	1,65	7.662	0.007
t1.6	Clutch size	1,65	0.513	0.476
t1.7	SD (random)			0.125

**Fig. 4** Hosts' behaviour at nests in three categories (treatment 1b, treatment 3 and control) as video recordings revealed. Measured variables were: **a** pecking — number of egg pecking, **b** inspection — time spent with clutch inspection (seconds), **c** sitting — sitting on the eggs (seconds) and **d** rotation — time spent by rotation of the eggs (seconds). All values are rates and calculated per hour. The box plot shows the median (*central horizontal line*), 75th and 25th percentile (*top and bottom of the box*) and the maximum and minimum values (*top and bottom whisker*), respectively. Minor outliers, observations 1.5 \* interquartile range (IQR) outside the central box, are shown by dots, and major outliers, observations 3.0 \* IQR outside the central box, are indicated by asterisks



423 despite a lack of rejection response, hosts were able to recog- 431  
 424 nize the parasitism took place during incubation. Similar rates 432  
 425 of pecking activity was seen in both treatment categories 433  
 426 suggest that some of the host individuals are capable of 434  
 427 detecting foreign eggs, even if they do not reject them (cf. 435  
 428 Antonov et al. 2009). Birds in the control group also scanned 436  
 429 clutches prior to settling for incubation, most likely to allow 437  
 430 the possibility of parasitic vs. own egg discrimination at each 438

visit to the nest. Although sample sizes in our video recordings 431  
 were relatively small, these data clearly showed that great reed 432  
 warblers in later stages of experimental parasitism also 433  
 inspected their clutches at least as intensively as did birds in 434  
 earlier parasitism or, at the control nests. 435

Some of the hosts that were exposed to later parasitism, 436  
 were able to recognize the foreign eggs clearly, as shown by 437  
 high pecking rates, but they did not proceed to egg rejection 438

t2.1 **Table 2** Results from the per-  
 t2.2 mutational ANOVA, assessing  
 the effect of treatments 1b, 3, and  
 t2.3 the control, regarding the fre-  
 t2.4 quency of egg pecking, clutch in-  
 t2.5 spection, incubation and rotation  
 t2.6 of eggs in nests of great reed  
 warblers

Response		df	SS	MS	Iteration no.	P
Egg pecking	Category	2	281.34	140.61	3,893	0.061
	Residuals	23	1,694.35	73.66		
Clutch inspection	Category	2	632.57	316.28	1,071	0.108
	Residuals	23	2,858.92	124.3		
Sitting	Category	2	153,807	76,904	198	0.616
	Residuals	23	2,852,462	124,020		
Rotation	Category	2	3,047	1,523.48	5,000	0.028*
	Residuals	23	10,637	462.26		
Rotation without the outlier	Category	2	926.4	463.22	2264	0.140
	Residuals	22	5,107.6	232.4		

t2.15 \*Non-significant effect when a  
 t2.16 statistical outlier data point was  
 t2.17 removed (see section "Rotation  
 without the outlier" for details)



439 during incubation. Earlier studies revealed that mimicry of the  
440 parasitic eggs influences host responses to brood parasitism  
441 (e.g., Davies 2000; Aviles 2008; Stoddard and Stevens 2010).  
442 If mimicry is weak, it causes greater responses (i.e., more  
443 rejections) to cuckoo parasitism, but when mimicry is strong,  
444 it causes poorer responses in the great reed warbler (e.g.,  
445 Cherry et al. 2007). Great reed warblers reject highly non-  
446 mimetic eggs at the highest rates (close to 100 %) at clutch  
447 completion or in the first few days just after completion  
448 (Moskát 2005). However, our experimental parasitic eggs  
449 could be regarded as moderately mimetic, and their rejection  
450 rates are about 30–50 % during the laying stage (Bán et al.  
451 2013). During incubation, the risk of natural cuckoo parasit-  
452 ism is low in this host species (Moskát 2005) and the cost of  
453 such late parasitism is also low (because later laid cuckoo eggs  
454 are less likely to hatch, Birkhead et al. 2011), so, probably,  
455 there is no pressure for hosts to keep egg discrimination  
456 responses at high rates. When the hosts do eject a mimetic  
457 parasitic egg, there is always a chance that they might mistake  
458 their own egg for the foreign egg (ejection error) or damage or  
459 destroy one or more own eggs accidentally (ejection cost, see  
460 Davies and Brooke 1988; Stokke et al. 2002). In turn, as  
461 incubation progresses, the realized fitness value of the clutch  
462 increases that compounds the costs of rejection errors and  
463 rejection mistakes when hosts damage or destroy their own  
464 eggs. Although ejection cost was rare in the present study (see  
465 Results), several previous studies on this host population  
466 showed ejection errors and costs (e.g., Moskát 2005; Moskát  
467 and Hauber 2007), which may select against egg ejection.  
468 Together with the decreasing chances of re-nesting  
469 before migration, the progress of the breeding season  
470 should therefore lower the rate of egg rejection during the  
471 later, incubation stage of the breeding cycle, compared to the  
472 earlier laying stage.

473 Studies on the effect of nesting stage on egg rejection  
474 behaviour in hosts of brood parasites have revealed diverse  
475 patterns. For example, five songbird species, including the  
476 reed warbler (*Acrocephalus scirpaceus*), rejected the non-  
477 mimetic model cuckoo eggs at similar rates, when experimen-  
478 tally parasitized during either laying or incubation (Davies and  
479 Brooke 1989). However, the latency of rejection was longer  
480 when experimental parasitism took place earlier, at the begin-  
481 ning of laying. In contrast, great reed warblers showed a lower  
482 frequency of egg rejection. In response to natural parasitism  
483 by cuckoos, in the incubation stage, relative to the laying stage  
484 (Moskát 2005). In a population of the red-backed shrike  
485 (*Lanius collurio*), that had been abandoned by the cuckoo,  
486 breeding stage had no effect on egg rejections, irrespective of  
487 the level of mimicry. However, the method of rejection of  
488 mimetic eggs changed from desertion during the laying peri-  
489 od, to ejection during the incubation period (Moskát and Fuisz  
490 1999). Cedar waxwings (*Bombycilla cedrorum*) typically  
491 ejected foreign eggs in the early stage of breeding (laying),

492 but showed tendency to accept them during the late stage  
493 (incubation) (Rothstein 1976), although this pattern was un-  
494 usual among several different host species of the brown-  
495 headed cowbird (*Molothrus ater*) (Rothstein 1976).  
496 Underwood and Sealy (2006) also failed to find a breeding-  
497 stage specific effect on egg rejection frequency in the Eastern  
498 warbling vireo (*Vireo gilvus*), a common host of the brown-  
499 headed cowbird. Some of other cuckoo hosts and potential  
500 hosts followed this pattern of egg rejection (Davies and  
501 Brooke 1989; Moksnes et al. 1991; Moksnes 1992; Grim  
502 et al. 2011), but there are examples when hosts of brood  
503 parasites showed reduced rejection in incubation in relation  
504 to laying (Moksnes et al. 1991; Lotem 1995), either due to the  
505 decrease in the threat of parasitism in this stage or the in-  
506 creased cost of breeding in the later stages (Røskaft and  
507 Moksnes 1998).

508 Hauber et al. (2006) documented that, following the suc-  
509 cessful ejection of a highly non-mimetic parasitic egg, great  
510 reed warblers possess a better egg recognition ability, and  
511 eject more mimetic eggs than without this "training" on the  
512 parasitic eggs. In our study we did not observe a similar effect,  
513 however, our experimental design in the present study differed  
514 in several respects from that of applied in Hauber et al. (2006)  
515 (e.g. that study varied the type of mimicry, from poor to  
516 intermediate, but experimental parasitism was mostly  
517 conducting during the laying period). The variation in the  
518 avian-perceivable mimicry component of an egg is regarded  
519 as a key factor that motivates hosts to engage in egg rejection  
520 behaviours (Soler et al. 2012a).

521 In this study, we discovered that hosts consistently accept-  
522 ed moderately mimetic parasitic eggs in the early incubation  
523 stage, compared to higher rates of rejection in the laying stage.  
524 On the one hand, cuckoos would benefit from this temporally  
525 variable pattern of host rejection if they parasitized great reed  
526 warbler nests in the early incubation stage. On the other hand,  
527 such late cuckoo parasitism might cause reduced hatchability  
528 of cuckoo eggs (Birkhead et al. 2011). Even if the cuckoo egg  
529 successfully hatched, there would a risk of unsuccessful ejection  
530 of already hatched and larger nestmates, as the younger  
531 cuckoo chick might be too weak to displace the hosts' growing  
532 chicks from the nest (Molnár 1939; Moskát and Hauber  
533 2010); and so the cuckoo chicks would pay the variable costs  
534 of nestmate eviction attempts (Anderson et al. 2009), and of  
535 the co-habitation with host nestlings (Hauber and Moskát  
536 2008; Geltsch et al. 2012). Therefore, late cuckoo parasitism  
537 should be selected against; indeed, it occurs rarely in natural  
538 parasitism: with observations showing that the risk of cuckoo  
539 parasitism during the last days of laying is about 30 %, where-  
540 as it falls to 4 % during early incubation (Moskát 2005).

541 Repeated brood parasitism may have cumulative fitness  
542 impacts and complex evolutionary effects on hosts of brood  
543 parasites, and their anti-parasitic responses. If long-term, re-  
544 peated risk of parasitism is distributed non-randomly among



545 hosts, then certain individuals suffer from a high risk of  
 546 repeated parasitism, while others may serially escape from  
 547 parasitism (Grim 2002; Hauber et al. 2004; Hoover et al.  
 548 2006; Hoover and Hauber 2007; Molina-Morales et al.  
 549 2012). In the present study we tested the short-term effects  
 550 of repeated brood parasitism by field experiments, and re-  
 551 vealed reduced egg rejection responses in the incubation stage  
 552 compared to the egg laying stage. However, our results also  
 553 showed that the difference in the behavioural outcomes of  
 554 acceptance or rejection was not related to a lack of opportunity  
 555 or any cognitive constraint, during repeated brood parasitism.  
 556 Instead, lack of rejection in repeated parasitism can be  
 557 regarded as the temporal consequence of later brood parasit-  
 558 ism, occurring during the incubation stage. We conclude this  
 559 because video-records showed that hosts were able to recog-  
 560 nize the parasitic eggs in late parasitism, as was indicated by  
 561 pecking, which did not result in broken eggs (Soler et al. 2002,  
 562 2012a; Honza et al. 2007; Antonov et al. 2008, 2009;  
 563 Pozgayová et al. 2011). Accordingly, our study illustrates an  
 564 example of the previously hypothesized phenomenon that  
 565 some hosts may recognize more eggs than they reject (Lyon  
 566 2003; Moskát and Hauber 2007; Soler et al. 2012b). We  
 567 suggest that further field studies on hosts' egg discrimination  
 568 should focus on how variation in the behavioural display of  
 569 acceptance vs. rejection, as an evolutionary adaptation, is  
 570 affected by intrinsic and extrinsic factors of the hosts.  
 571 Experiments on repeated brood parasitism shall continue to  
 572 offer valuable tools to reveal the sensory and ecological com-  
 573 ponents of foreign egg recognition behaviour in general  
 574 (Hauber et al. 2006; Peer and Rothstein 2010; Samas et al.  
 575 2011).

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581 **Ethical standards** The Middle- and Lower-Danube-Valley Inspectorates  
 582 for Environmental Protection, Nature Conservation and Water  
 583 Management provided permission for research. The authors declare that  
 584 their experiments performed in this study comply with the laws of Hungary.  
 585

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