1 **Post ejection nest desertion of hosts of avian brood parasites; a**

2 **second defence mechanism or avoiding reduced reproductive**

3 **success?**

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24 Abstract

25

26 Avian hosts of the common cuckoo (*Cuculus canorus)*, a brood parasite, develop anitiparasite

27 mechanisms to increase their reproductive success. Ejection of the parasite egg or desertion of

28 the parasitized nest are the most typical adaptations in response to brood parasitism. Some

29 great reed warblers (*Acrocephalus arundinaceus*), a highly parasitized host of the common

30 cuckoo, showed both mechanisms: just after the successful ejection of the parasite egg they

31 deserted their nests. We studied if such cases of post ejection nest desertion are related to

32 brood parasitism. We experimentally parasitized clutches having five or three host eggs by

33 two brown eggs. We found that post ejection nest desertion frequently occurred in the second

34 category, but it was almost absent when bigger clutches were manipulated. The same

35 phenomenon was also found when clutches just completed with five eggs and clutches in the

36 laying stage with three eggs were reduced by two eggs. A logistic regression model revealed

37 that only clutch size affected nest desertion in our experiments. For this reason we stated that

38 post ejection nest desertion is not a second antiparasite mechanism might serve for a

39 redundant antiparasite defence, but it is rather a reaction to decreased clutch size.

40
41 Key words: cuckoo, great reed warbler, antiparasite defense, clutch size, clutch reduction
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43   The common cuckoo (*Cuculus canorus*, hereafter 'cuckoo') is a well-known brood parasite,

44   which parasitizes more than a hundred small passerine species breeding in the Palearctic

45   (Wyllie 1981, Davies 2000, Payne 2005). The coevolutionary processes between cuckoos and

46   their avian hosts are typically explained as a coevolutionary arms race (Dawkins and Krebs

47   1979, Davies 2000, Krüger 2007), which leads to adaptations and counteradaptations between

48   the hosts and the cuckoo (Davies and Brooke 1988, Moksnes et al. 1991). The host having the

49   strongest adaptive mechanism will eventually win the coevolutionary race, and escapes from

50   brood parasitism (e.g. Lovászi and Moskát 2004). Brood parasitism causes a high cost for the

51   hosts' breeding success and therefore hosts develop defence mechanisms against brood

52   parasitism (Davies 2000). The most prominent antiparasite adaptations are based on the

53   recognition of the parasite eggs (Hauber and Sherman 2001). There are three known

54   mechanisms of egg rejection (Rothstein 1974): A host detects a parasitic egg and (i), as a

55   consequence, it deserts the nest, or (ii) it ejects the parasitic egg or (iii) it buries the parasitic

56   egg in the nest. Hosts' antiparasite defence selects for mimetic eggs in cuckoos, resulting in

57   similar eggs of the brood parasite to that of the host species. Highly mimetic parasitic eggs

58   typically have lower chance of being rejected by hosts than non-mimetic eggs (Davies 2000).

59   However in some situations hosts may desert their nests after successfully ejecting the

60   parasitic eggs. Nest desertion after egg ejection (we term it as 'post ejection nest desertion') is

61   rare, but not an unknown phenomenon (Antonov et al. 2008) in brood parasitism studies,

62   however, there is almost no knowledge about the functional aspects of this behavior. To our

63   knowledge, it has never been studied if this phenomenon is related to brood parasitism as part

64   of hosts' antiparasite defense or has another role. Here, we demonstrate an experiment on a

65   cuckoo host where we compare nest desertions after clutch reduction in non-parasitized nests

66   and following the ejection of parasitic eggs.

67   There are several mechanistic explanations why nest desertion may occur. In hosts of

68   brood parasites, it could be a form of antiparasite defence. A study at host nest desertion

69   showed that brown-headed cowbirds' (*Molothrus ater*) activity near the hosts' nest and egg

70   removal by the female cowbird may lead to nest desertion by the host (Strausberger and

71   Burhans 2001). Desertion could be a response to partial clutch or brood reduction and with

72   that reduced value of the clutch or brood. Consequently, nest desertion can be the

73   consequence of nest predation (Hill and Sealy 1994). According to the parental investment

74   theory parents try to find an optimum between costs and reproductive success. If the benefits

75   deserting the nest are bigger than the benefits from the current breeding attempt, the parents

76   will desert the nest according to the parental investment theory (Pianka 1976; Sargant and

77   Ghross 1985; Winkler 1991). Consequently, sometimes only one of the parents deserts

78   (Székely et al. 1996, Valera and Hoi 1997, van Dijk et al. 2007).   Another antiparasite

79   defence mechanism, egg ejection, is much more specific to brood parasitism, while nest

80   desertion is a pre-existing behaviour, among others, a response to nest predation (Hosoi and

81   Rothstein 2000). However, egg ejection shows a close relationship with nest sanitation

82   behaviour (Rothstein 1975). Birds eject foreign objects (Ortega and Cruz 1988, Moskát et al.

83   2003, Guigueno and Sealy 2009), like leafs, small twigs, artificial object and broken, or debris

84   eggs (Underwood and Sealy 2006) from nests. However, after successful ejection of the

85   foreign objects there is probably no need to desert the nest.

86   We carried out experimental parasitism on a great reed warbler (*Acrocephalus*

87   *arundinaceus*) population in Hungary, to understand why nest desertion after ejection of the

88   parasitic egg occurs. In Hungary the great reed warbler is unusually highly parasitized by

89   cuckoos (over 60%; Moskát and Honza 2002). A study on host rejection behaviour towards

90   parasitic eggs showed 66% acceptance, 12% ejection, 20% desertion and 2% egg burial

91   (Moskát and Honza 2002), and nest desertion following the successful ejection of a cuckoo

92   egg has already been observed in this population (C. Moskát, unpublished). We hypothesised

93   that 'post ejection nest desertion' is a new form of hosts' antiparasite defence. If hosts are

94   uncertain if egg ejection was successful, they could still escape from brood parasitism and its

95   consequences by deserting the nest. By building a new nest hosts might lower the chance of

96   being found by the cuckoos and get parasitized again. We predict a higher desertion rate of

97   experimentally parasitized clutches just after the successful ejection of the parasitic eggs than

98   when clutches are reduced without any incidents of parasitism. Alternatively, we also

99   hypothesised that nest desertion after a successful ejection is due to a reduced clutch size, so it

100   is not the consequence of brood parasitism. In this case we predict a higher nest desertion rate

101   following clutch reduction than just after the ejections of parasitic eggs.

102

103   Methods

104

105   *Study site and species*

106   The research was performed in the surroundings of the village Apaj (47°07'N; 19°06'E) and

107   the town Kunszentmiklós (47°02'N; 19°08'E), in central Hungary, ca. 40-60 km south of

108   Budapest. We carried out our experiments on the great reed warbler in a ca. 20 x 35 km area,

109   a part of an intensive system of small channels between 14 May and 14 June 2009. This

110   species, is a host of the cuckoo, is heavily parasitized in the area (see above).

111   To find great reed warbler nests, we systematically searched the 2-4 m wide channel-

112   side reed beds (*Phragmites australis)* once or twice a week. New nests were signed by small

113   pieces of yellow tags at the edge of the reeds and coordinates of the nests were fed into a GPS

114   (GPS 60, Garmin Co., Olathe, Kansas, USA) to help finding the nests later. To keep cuckoo

115   parasitism on experimental nests as low as possible we chose channel sections with low

116   density of trees on the banks or with no trees at all, which might serve as vantage points for

117   cuckoos when looking for suitable nests (Moskát and Honza 2000). The nests we used for

118   experiments were freshly made or already contained a few eggs. In this way we could follow

119   the process of egg laying and avoid using nests that contained cuckoo eggs before. (For more

120   details of the study area see Moskát and Honza 2000, and Moskát et al. 2009 for more details

121   of the basic methods.)

122   For treatments we manipulated two host eggs by painting overlapping spots on the

123   eggshell (covering at least 98 percent of the egg to induce a high ejection rate), which we

124   placed afterwards into another host's nest. The eggs of the great reed warbler are suitable for

125   experimental parasitism due to their similar size as the cuckoo eggs (Török et al. 2004). As a

126   previous study revealed that using plastic eggs caused extra costs for the hosts when ejected

127   the plastic eggs by making a small hole for puncture ejection when compared to real eggs

128   (Honza and Moskát 2008).

129   As multiple parasitism is relatively common in our study area (54% of the cuckoo

130   eggs were found in multiple parasitized great reed warbler nests, Moskát and Honza 2002),

131   we chose for manipulation of two non-mimetic parasitic eggs, instead of one, getting higher

132   rejection rates than against one non-mimetic egg, (Honza and Moskát 2005). In order to study

133   'post ejection nest desertion' experimentally, we tried to maximize the frequency of ejections

134   to trigger the desertion need of the hosts.

135   We mention that in the year of the study we observed 2 natural cases of post ejection

136   nest desertions out of 13 clutches where the single cuckoo egg was ejected. In the first case

137   hosts ejected the cuckoo egg with rejection cost (sensu Stokke et al. 2002), i.e. 3 host eggs

138   were lost together with the cuckoo egg. In the second case the clutch contained one cuckoo

139   egg and one host egg when the cuckoo egg was ejected. Interestingly, in both of these cases

140   clutch size was reduced to only one host egg.

141

142   *Experimental treatments*

143

144   We experimentally manipulated clutches in two stages of egg laying: (I) clutches containing 5

145   eggs (typically these clutches were complete), which is the modal clutch size of great read

146   warblers in the study area (Moskát et al. 2008) and (II) clutches containing 3 eggs (typically

147   representing the middle of the laying process). We carried out experiments on the days when

148   the fifth or third eggs were laid, depending on the two categories. In this way we could find

149   out the impact of clutch size on post ejection nest desertion.

150   Kosciuch et al. (2006) studied nest desertion in the Bell's vireo (*Vireo bellii*), which is

151   the host of the brown-headed cowbird. They showed that cowbird eggs caused desertion

152   because of the reduction of hosts' own eggs in the clutch. However, if the original vireo's eggs

153   were put back into nest on the next morning after exchanging two host eggs by two cowbird

154   eggs, hosts failed to desert their nests. Similarly, we also applied a treatment, when we placed

155   back hosts original eggs, but just after the ejection of the parasitic eggs. We expected that

156   hosts might watch their complete clutches again, so they would not desert. Additionally we

157   also monitored control clutches, which were checked with the same frequency as

158   experimental nests.

159   We summarized the different treatments and the controls below (see also Figure 1).

160   **(i)**   "Clutch reduction from 5 to 3 eggs": on the day when the 5th egg was laid into

161   clutch, we took 2 eggs out, selected by chance, to reduce the clutch to 3 eggs.

162   **(ii)**   "Swapping at clutch size = 5": on the day when the 5th egg was laid into clutch,

163   we took 2 eggs out, selected by chance. We painted two great reed warbler eggs

164   from another clutch dark brown (overlapping spots with a diameter between 4 and

165   5 mm, covering the eggshell for at least 98%) and placed them into the nest just

166   after the two own eggs were removed. For all painting experiments we used M-

167   size dark brown waterproof fibre pens (Faber-Castel OHP-Plus permanent, size

168   code: 1525; colour code: 78).

169   **(iii)**   "Clutch reduction from 3 to 1 egg": on the day when the 3rd egg was laid into

170   clutch, we took 2 eggs out, selected randomly, to reduce the clutch to 1 egg.

171   **(iv)**   "Swapping at clutch size = 3": on the day when the 3rd egg was laid into clutch,

172   we took 2 eggs out, chosen randomly, and placed two great reed warbler eggs

173   taken from another clutch. We painted these eggs dark brown prior to the

174   experiment using overlapping spots with a diameter between 4 and 5 mm. These

175   spots covered the eggshell surface for at least 98%.

176   **(v)**   "Swapping and restoration": As (iv), but after ejection of the two parasitic eggs we

177   placed back the two original host eggs, which were taken out when the experiment

178   started. To reduce the chance that hosts could watch their clutches just with

179   reduced clutch size, we checked nests twice a day, instead of the usually one

180   checking per day (c.f. Moskát et al. 2008, 2009).

181   **(vi)**   We also used nests for "control", where no eggs in these clutches were

182   manipulated, but nests were checked as for the other treatments.

183   We checked nest contents two times a day for all treatments (including the control

184 group). We checked nests for six consecutive days when no response was observed, or until

185 the nest was deserted (cold egg(s), no rotation of the eggs for three days). If the parasitic eggs

186 were ejected in treatments (ii), (iv) and (v), we also checked these nests after ejection for six

187 days, or until nest desertion. Video records revealed that in great reed warblers the females

188 were typically responsible for nest checking and egg rejection behaviour (Pozgayová et al.

189 2009), so hosts' reactions mainly attributable to females in this species.

190 We only used nests for our results that were not depredated, parasitized naturally by cuckoos

191 or destroyed by storms.

192

193 <u>Statistical analyses</u>

194

195 We constructed a set of multinomial logistic regression models in SPSS ver. 17 (SPSS Inc.) to

196 evaluate what parameters affect on nest desertion. In the full model we included 'nest

197 desertion' as the dependent variable, 'laying date', and 'clutch size at experiment' as covariates,

198 and the 'usage of brown eggs' as fixed factor. Laying date was involved into the full model, as

199 Lotem et al. (1992) revealed age-dependent structure of laying in the oriental reed warbler

200 (*Acrocephalus orientalis*, previously considered as the subspecies of the great reed warbler).

201 We defined laying date as the laying of the first egg in clutch, where laying date of the earliest

202 clutch was defined as 1. 'Clutch size at experiment' showed if the experiment was started on a

203 clutch with 5 (in two cases 6) or 3 eggs. The 'usage of brown eggs' shows if parasitic eggs

204 (conspecific eggs painted dark brown, see above) was applied for the clutch or not. Model

205 selection was based on Akaike information criteria (Burnham and Anderson 2002, Anderson

206 2008), corrected for small sample bias.

207

208 Results

209

210 Our results revealed that hosts did not desert their clutch when number of eggs in their nests

211 were reduced from 5 to 3 (treatment i), and if they ejected the brown eggs (treatment ii) only 2

212 nests were deserted. However, in these nests we observed some yolk on the eggs suggesting

213 that hosts broke an egg when ejected the brown eggs, and consequently they deserted the eggs

214 with glued eggs. No other egg breakage was observed in the other treatments and controls.

215 When we started our experiments at clutch size = 3, both desertion rate (treatment iii), and

216 post ejection nest desertions (treatment iv) increased (Table 2). We found a significant

217 difference (Fisher's exact test, 2-tailed, P = 0.042), when the ratio of nest desertions and

218 acceptances (combined with corresponding values for post ejection nest desertions) was

219 compared in the 5- and 3-egg categories (2 /22 for treatments (i) and (ii), and 9/18 for

220 treatments (iii) and (iv) in Table 1). The variant of the swapping experiment (treatment v)

221 gave similar result to treatment iv (acceptances vs. rejections: Fisher's exact test, 2-tailed: P <

222 1.000; post ejection nest desertions vs. no desertion following ejections: Fisher's exact test, 2-

223 tailed: P = 0.6380). No clutch was deserted in the control group of nests within the 6-day

224 monitoring period.

225   The model, which included all of our variables (Model 4; Table 2), revealed that

226 'clutch size at experiment' had significant effect (P = 0.004) on nest desertions. All other

227 models revealed the same effect of this variable (0.005 < P <0.018), regardless if the other

228 covariates and the factor were included or not. All of the other parameters had non-significant

229 effects in any of the models ('laying date': 0.080 < P = 0.095, 'using of brown eggs': 0.341 <

230 P < 0.507). The full model (Model 4) and Model 3 showed the worst parameters of model

231 evaluation (Table 1). The smallest Akaike information criterion was revealed for the model

232 when only the covariate 'clutch size at experiment' was included for independent variables

233 (Model 1), and the corresponding Akaike weight indicated that the likelihood that this model

234 was the best (w_1 = 0.97). Model probability was much smaller for Model 2 (0.03), so only

235 Model 1 was acceptable. This clearly led to our conclusion that post-ejection nest desertion

236 was mainly (P = 0.018) affected by the clutch size at experiment.

237

238 Discussion

239

240 Our results clearly supported that post ejection nest desertion was due to a reduced clutch size

241 and not related to brood parasitism. We found nest desertions when experiments were started

242   from three eggs, but no desertions were found when clutch size was higher (five egg

243   clutches). This behaviour could be explained by the higher cost invested into clutches with

244   higher number of eggs. Hosts' desertion rate might decrease when they have already invested

245   more in egg laying (for example when they laid five eggs instead of three). Similarly, reduced

246   desertion rates in hosts of brood parasites were found at the end of the breeding season

247   (Alvarez 1999). Although we did not find this effect in our study (due to early research), it

248   has never been shown by any previous study on cuckoo parasitism in our study area (e.g.

249   Moskát and Honza 2002). Another study on great reed warblers revealed that hosts rejected

250   less parasitic eggs when chance for rejection costs or errors were higher, i.e. when clutch size

251   was higher (Moskát and Hauber 2007).

252   Alternatively, we could explain this result based on cognitive backgrounds. The two

253   most important mechanisms for egg recognition are based on the discordancy of the eggs

254   (Rothstein 1974), and the memory-template of their eggs, which is the type of true recognition

255   (Lahti and Lahti 2002). Previous studies supported that great reed warblers use both the

256   discordancy (Cherry et al. 2007, Moskát et al 2008) and the true recognition (Hauber et al.

257   2006, Moskát and Hauber 2007) mechanisms for discrimination of the parasitic eggs. When

258   clutch size consists of one natural host egg and two parasitic eggs, as in one of our

259   experimental treatments (treatment iii), the parasitic eggs are dominated in the clutch, which

260   may cause difficulties in egg recognition for hosts using the discordancy mechanisms. When

261   clutch size is five, including two parasitic eggs, the parasitic eggs are in the minority in the

262   clutch, giving better conditions for egg recognition based on discordancy.

263   Our results revealed that some of the hosts did not desert following the ejection of the

264   parasitic eggs in treatments (iii), but deserted when ejected the parasitic eggs quickly. This

265   result also supported clutch size dependent desertion. Consequently, hosts deserted when

266   clutch size was reduced from three to one after the ejection of the two parasitic eggs, but did

267   not desert when clutch size increased to four or five just before the ejection of the parasitic

268   eggs (raw data, not discussed here).

269   We tried to eliminate clutch size effect by introducing hosts original eggs just after

270   they rejected the two parasitic eggs. Although this procedure proved to be useful in the hosts

271   of the brown headed-cowbird, it had no effect on hosts' rejection rates when compared either

272   with treatments (ii) or (iv). In this way we could not eliminate clutch size effect although we

273   checked nests twice a day. This result suggests that great reed warblers could have recognized

274   the parasitic eggs quickly. For that we replaced the original eggs probably too late, so the

275   hosts already made their decisions to desert the nests.

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370

371 Table 1. Hosts' responses to experimental treatments: (i) "clutch reduction from 5 to 3 eggs";

372 (ii) "swapping at clutch size = 5", i.e. swapping 2 host eggs with 2 parasitic conspecific, eggs

373 (painted dark brown); (iii) "clutch reduction from 3 to 1 egg"; (iv) "swapping at clutch size =

374 3", i.e. swapping 2 host eggs with 2 parasitic, conspecific eggs (painted dark brown); (v)

375 "Swapping and restoration": i.e. swapping 2 host eggs with 2 parasitic, conspecific eggs

376 (painted dark brown), and just after the ejection of the brown eggs, hosts' original eggs were

377 set back into the nest; (vi) controls.

378

Treatment	Acceptance (%)	Desertion (%)	Ejection (%)	Post ejection nest desertion (% of ejections)	n
(i)	100	0	n.a.	n.a.	12
(ii)	0	0	100	17	12
(iii)	58	42	n.a.	n.a.	12
(iv)	33	0	67	40	15
(v)	27	0	73	25	11
(vi)	100	0	n.a.	n.a.	19

379 n.a. = not applicable

380

381 Table 2. Logistic regression models exploring the effect of 'laying date' (LD), 'clutch size at

382 experiment' (CE) and 'using brown eggs' (BE) on 'nest desertion' (ND) of great reed warblers.

383 Models are ranked from the best to the worst based on Akaike information criteria (corrected

384 for small sample bias) (k = number of parameters, including all independent and the

385 dependent variables, AIC_C = Akaike information criteria, corrected for small sample bias, Δ_i

386 = $AIC_{C,i} - AIC_{C,min}$, w_i = Akaike weight, which is the likelihood that the single model with the

387 lowest AIC_c value is the best exploratory model).

388

Models		k	$AIC_{C,i}$	Δ_i	w_i
1	CE	2	10.41	0	0.97
2	CE + BE	3	17.27	6.86	0.03
3	CE + LD	3	31.07	20.66	3.17e-5
4	CE + BE + LD	4	42.11	31.70	1.27e-7

389

390

391   Legend to figures

392

393   Figure 1. Hosts' responses to different treatments: (i) "clutch reduction from 5 to 3 eggs"; (ii)

394   "swapping at clutch size = 5", i.e. swapping 2 host eggs with 2 parasitic conspecific, eggs

395   (painted dark brown); (iii) "clutch reduction from 3 to 1 egg"; (iv) "swapping at clutch size =

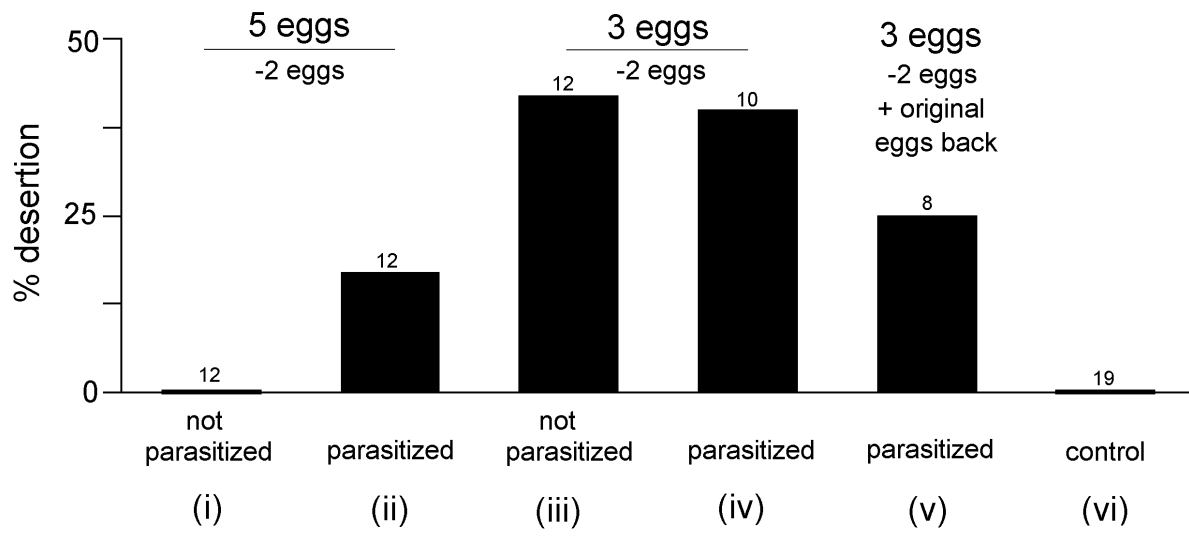396   3", i.e. swapping 2 host eggs with 2 parasitic, conspecific eggs (painted dark brown); (v) ...;

397   (vi) controls.

398

399

400   Figure 1.

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404